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# Bulletins of American Paleontology

*Begun in 1895*

NUMBER 362 AUGUST 20, 2002

# The Genus *Heliophyllum* (Anthozoa, Rugosa) in the Upper Middle Devonian (Givetian) of New York

by

William A Oliver, Jr.

and

James E. Sorauf

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# THE GENUS *HELIOPHYLLUM* (ANTHOZOA, RUGOSA) IN THE UPPER MIDDLE DEVONIAN (GIVETIAN) OF NEW YORK

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## ABSTRACT

Specimens of the genus *Heliophyllum* are among the most common components of the upper Middle Devonian coral fauna (Givetian; Hamilton Group and Tully Limestone) in New York State. Although these corals are abundant and widespread, examination of large numbers of specimens indicates that most of them belong in a single, variable species, *H. halli* Milne-Edwards and Haime, including both solitary and colonial forms. This study has resulted in the recognition of four subspecies of *H. halli*, the solitary *H. halli halli*, and three colonial subspecies, *H. halli confluens* (Hall), *H. halli bellonense* n. subsp., and *H. halli joshuense* n. subsp. The three colonial subspecies occur in restricted stratigraphic positions, each in a coral bed in which it is associated and intergrades with solitary *H. halli halli*.

Two additional species of *Heliophyllum* are recognized in the Hamilton, the small, solitary *H. cribellum* n. sp. and the dendroid branching *H. delicatum* Oliver and Sorauf. The former has been found only in the Centerfield Limestone, lower Ludlowville Formation; the latter is limited to the lower Deep Run Shale, Moscow Formation.

*Heliophyllum halli* flourished in muddy but well-oxygenated parts of the Hamilton sea floor because basal, rootlike structures (talons) and shape adaptations helped keep the living polyp from being overwhelmed by the mud. Septal carinae are thought to have helped anchor the polyps in their calices, perhaps making it easier for them to remove any sediment that accumulated on the oral surface.

*Heliophyllum cribellum* is common in the Centerfield Limestone, which represents a more calcareous, relatively stable sea floor, while *H. delicatum* seems to have adapted to a more muddy, subsiding sea floor by fast upward growth. However, both species were associated with solitary *H. halli halli*, a further indication of the great adaptability of this species.

## INTRODUCTION

*Heliophyllum* Hall is the most important and one of the most common rugose corals in the Middle Devonian of eastern North America. Hill (1957, p. 49) termed the eastern North American coral fauna "the *Heliophyllum* fauna" long before formal recognition of the currently accepted biogeographic realms and provinces (see Biogeography, p. 10). In New York, the genus ranges from the middle Emsian Bois Blanc Formation to the late Givetian Tully Limestone (see Text-fig. 1). The only known earlier, possible occurrence is in the Pragian or early Emsian Indian Cove Formation, Gaspé, Québec. One fragmental zaphrentid known from there may be a *Heliophyllum* (Oliver, 1997b, p. 318).

*Heliophyllum* is not restricted to eastern North America or to the Eastern Americas Realm (EAR) but this is its area of greatest abundance and longest stratigraphic record. It is present or common from Venezuela to the Hudson Bay Lowlands and from the Mississippi Valley (Kentucky, Missouri, Illinois) to the Appalachians (New York, southwest to the Virginias). Outside of the EAR, *Heliophyllum* occurs in northwest Africa and southwestern Europe and possibly other areas (see Oliver and Sorauf, 1988, p. 4–5).

This is the latest of several papers that we have published on aspects of the genus *Heliophyllum* (Sorauf and Oliver, 1976; Oliver, 1974, 1976, 1993b, 1997a, b; Oliver and Sorauf, 1988, 1994; Sorauf, 2001). Our main purpose is to describe, classify, and interpret typical *Heliophyllum halli* and allied forms from the Hamilton Group in New York. An additional purpose is to demonstrate the need for population studies of a species as variable as *H. halli*; we hope that our descriptions and illustrations will demonstrate the variation and provide a better basis for comparison with other taxa than has been available previously.

Most or all of our "populations" are Givetian in age although the earliest ones (Halihan Hill and Case Hill coral beds; population levels 1 and 2 on Text-fig. 1) may be Eifelian. Pre-Hamilton, Emsian-Eifelian, colonial *Heliophyllum* were described by Oliver (1976) and solitary forms were included in the microstructure study of Sorauf and Oliver (1976).

## ACKNOWLEDGMENTS

We are indebted to many people for help and cooperation during the course of this project. The late J. W. Wells, Ithaca, N.Y., contributed many Hamilton specimens from now-disappeared localities; P. H. Heckel, Iowa City, Iowa, gave many corals from his Tully Limestone study including most of our specimens of *H. halli bellonense*; and G. Kloc, Rochester, N.Y., gave us several beautifully prepared specimens for study and illustration of exteriors. M. Coen-Aubert, Brussels, Belgium, kindly sent new photographs of the neotype of *H. halli*; F. Debrenne and C. Perrin facilitated study of this specimen in Paris, France.

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Most of the more than one thousand thin sections used in this study were prepared by the late W. P. Pinckney, Jr., U.S. Geological Survey, Washington (USGS); some were made by K. Moore, USGS, and R. Jacyna, Binghamton University.

Most photomicrographs were processed and printed by D. Tuttle, Binghamton University, who also photographed many of the exteriors; additional photographs, especially of the colonial forms, were prepared by Pinckney and Moore. Text-figures were computer drafted by F. Marsh, Department of Paleobiology, USNM.

Field conferences with three individuals actively studying Hamilton biostratigraphy were useful and stimulating: G. C. Baird, State University College at Fredonia, New York; C. E. Brett, University of Cincinnati, Ohio, formerly at University of Rochester, N.Y.; and C. A. Ver Straeten, New York State Museum, Albany, New York.

W. T. Kirchgasser, State University of New York College at Potsdam, kindly sent an advance manuscript copy of his recent paper (2000) for our use in preparing Text-figure 1 and in making age assignments.

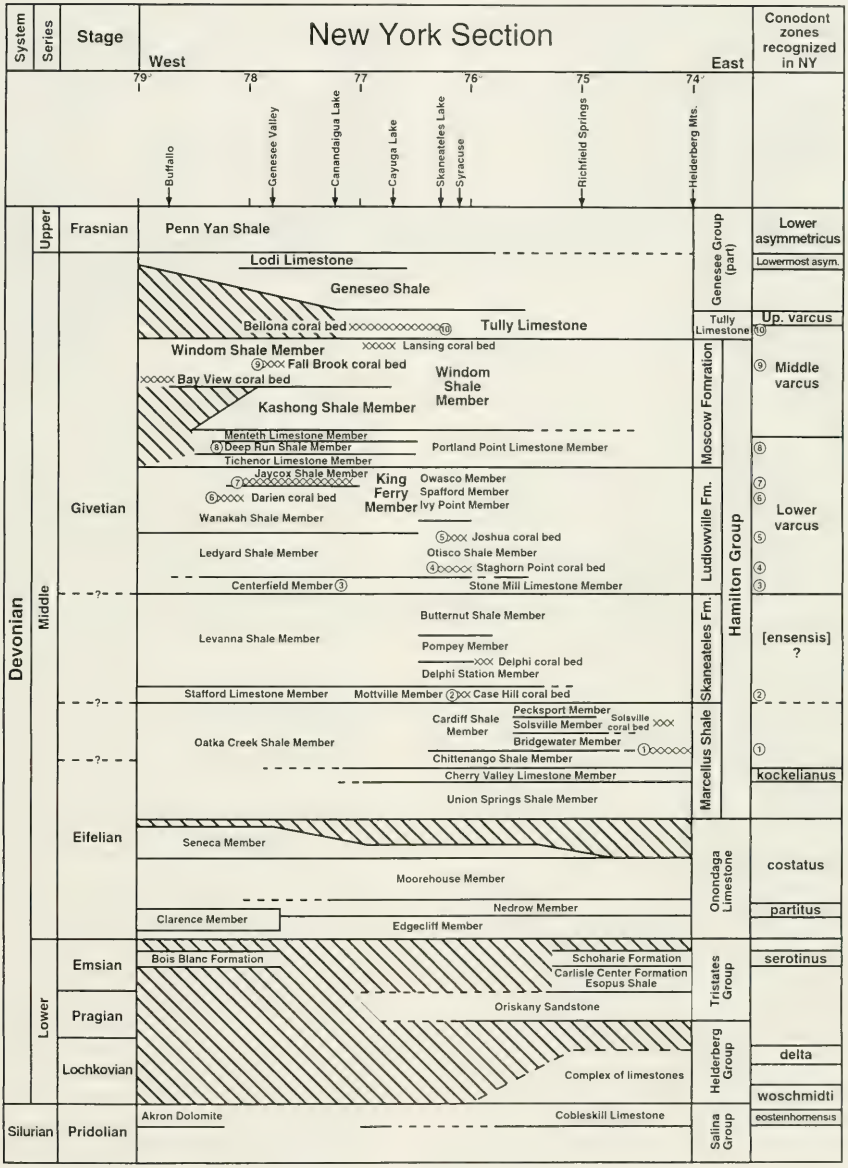
At various stages, the manuscript was critically reviewed by J. T. Dutro, Jr., USGS, Washington; R. J. Elias, University of Manitoba, Winnipeg, Manitoba, Canada; and ultimately by editor W. D. Allmon, Paleontological Research Institution; we thank them for their helpful suggestions.

## STRATIGRAPHY

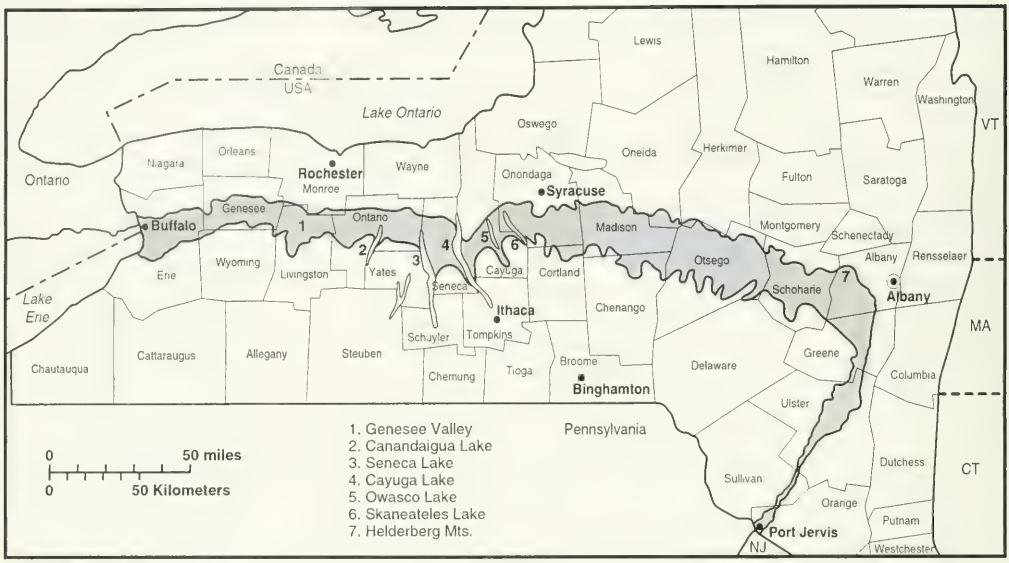
The Hamilton Group in New York and adjacent areas is a complex of facies ranging from continental red beds in eastern New York to offshore marine black shales in the west. Between these extremes are a spectrum of shallow marine facies, including gray calcareous shales with varied marine faunas and several coral beds (sedimentary units with corals as a significant component and of measurable thickness and extent) (Text-fig. 1). *Heliophyllum* is an important constituent of most of the coral beds, and is associated with other invertebrates in non-coral bed situations, especially in the upper half of the section (Centerfield and younger in Text-fig. 1). See Brett et al. (1983) for an extended discussion of coral associations in the Hamilton Group.

Hamilton strata were deposited during early and middle stages of the Acadian Orogeny. Sediments came from the east and, as the source area continued to rise, facies shifted westward so that coral beds and other environments favorable for corals are found in the east in the lower Hamilton and in the west in the upper Hamilton. Our systematic analysis is partly based on collections or "populations" (defined in Systematic Paleontology) of *Heliophyllum* from 10 stratigraphic levels. Text-figure 1 is simplified to show the stratigraphic position of these populations without the facies complexities of the Hamilton as a whole. However, the relative east-west positions of the coral beds in the figure show the general westward shift of facies with time. See Brett *et al.* (1990), Brett and Baird (1996), and included references for detailed stratigraphy and discussions.

The named coral beds (Text-fig. 1) were described and discussed by B. Smith (1912, 1935), Cooper (1933, 1943), Oliver (1951), Lane (1955), Grasso (1968, 1986), Heckel (1973), Brett *et al.* (1983), Mayer *et al.* (1994), and Ver Straeten (1994). Most of the populations of *Heliophyllum* that we analyzed are from the coral beds and are informally named after their source. Two populations, Centerfield and Deep Run, are not from well-developed coral beds, and are named for the stratigraphic unit in which they occur. Additional *Heliophyllum* specimens occur scattered through the Hamilton gray calcareous shale facies and in additional thin coral beds. The stratigraphy of the 10 populations is briefly noted in the following paragraphs (ascending stratigraphic order). Numbers 1 to 10 identify the populations in Text-figure 1 and in the systematic descriptions. All map quadrangles (Quads.) are from the 7.5 minute series of the U.S. Geological




Text-figure 1.—Generalized diagram of Lower and Middle Devonian stratigraphic units in New York. Series and stages are indicated on the left. The position of the Eifelian-Givetian boundary in the Middle Devonian is uncertain. The right-hand column indicates the positions of the standard conodont zones recognized in New York (updated following Kirchgasser, 2000). The circled numerals on the left side of the conodont zone column mark the stratigraphic levels of *Heliophyllum halli halli* populations 1 to 10; the same symbols on the main part of the diagram show the level and approximate west-east position of the source units. Unit 1 is the Hallihan Hill coral bed; unit 7 is the Jaycox Member. Greens Landing coral bed; other source units are labeled on the diagram. Modified from Oliver (1993a, fig. 1).




Text-figure 2.—Index map of New York showing the approximate outcrop area of Middle Devonian strata. It is impractical to show the 7.5 minute quadrangle boundaries at this scale but the counties, some of the principal cities, and seven regional reference points are labeled as an aid in finding the approximate positions of collection localities mentioned in the text and the Appendix. Modified from various small-scale outline maps of the New York State Geological Survey.

Survey. The quadrangles are too small to be shown on the map (Text-fig. 2) but citation of counties and other geographic features that are shown, gives a general location.

1. *Halihan Hill.*—Cooper (1933) first reported a coral bed in the lower Marcellus (now Mount Marion) Formation at two localities west of Albany, in the Schoharie Valley (Schoharie County) and northern Helderberg Mountains (Albany County) naming it the "*Meristella*-coral zone" after its principal components at these localities. Later, Cooper (1943) noted two additional exposures 55 km to the south in the Mount Marion-Kingston area, Ulster County. Lane (1955) described Cooper's four exposures and additional ones in the Schoharie-Helderberg area, and showed that in this northern area, the coral bed was essentially continuous for an east-west distance of some 20 km but that the bed did not appear in any of the numerous outcrops in the 55 km between the Helderberg and Mount Marion localities. Lane noted that the corals in this bed are markedly smaller than those of other Hamilton coral beds and that the thickness of the coral bed varies from 0.3 to 0.6 m (Lane, 1955). Ver Straeten (1994) gave the coral bed its geographic name from Halihan Hill, northwest of Kingston (Kingston West Quad.), near the two southern Cooper-Lane localities and just north of a new roadcut exposure. Ver Straeten's detailed stratigraphy fully supported Lane's earlier conclusion that the northern and southern outcrop clusters were in the same stratigraphic position. The Halihan Hill bed is late Eifelian or early Givetian in age, more likely the latter (see below and discussion in Kirchgasser, 2000).

2. *Case Hill.*—The Case Hill coral bed was described by Grasso (1968, 1986) as a limestone "abounding" with rugose and tabulate corals (dominated by *H. halli*), within the Mottville Member, Skaneateles Formation. The unit is approximately 2.5 m thick in the area from Lords Hill southeast to the south side of Bare Mountain (South Onondaga and Otisco Valley Quads., Onondaga County). The Mottville is either late Eifelian or, more likely, early Givetian in age (Kirchgasser, 2000).

3. *Centerfield.*—The Centerfield Member at the base of the Ludlowville Formation is the most widespread of the coral-bearing units in the Hamilton. It is one of the key units used by Cooper (1930, 1933–34) to divide the Hamilton into the four formations that are still widely recognized. The Centerfield is a mixture of thin limestones and calcareous shales, locally

almost a coral bed, but with a rich and varied assemblage of marine fossils. The unit extends from Erie County in the west to the Onondaga Valley in central New York (Onondaga Co.), some 200 km; corals are present to very common over much of this distance. The thickness of the coral-bearing beds is commonly 1 to 2 m. The small, commonly ceratoid-cylindrical *Heliophyllum cribellum* n. sp. is associated with solitary *H. halli* in the Centerfield. The member contains Lower *varcus* Zone conodonts, so this and all younger populations are Givetian or younger in age.

4. *Staghorn Point.*—The Staghorn Point coral bed is within the Otisco Shale Member of the Ludlowville Formation, approximately 15 m above the Centerfield Member. The bed consists of solitary rugose corals, a few tabulate corals, and little else other than shale matrix; it is as much as 3.5 m thick and extends for more than 29 km from the most spectacular exposure along the east side of Skaneateles Lake (Spafford Quad.) eastward to the Butternut Creek Valley (Jamesville and Tully Quads.) in Onondaga County. The most complete description of the unit is by Oliver (1951). It is Givetian in age.

5. *Joshua.*—The Joshua coral bed is approximately 30 m above the Centerfield Limestone Member and 12 m above the Staghorn Point coral bed in the Otisco Shale (Text-fig. 1). The Joshua occurs in the same general area as the Staghorn Point (Onondaga Co.) and is similar in being crowded with solitary rugose corals. However, it is thicker, up to 15 m, and extends only 14 km from Skaneateles Lake to Case Hill (Spafford and South Onondaga Quads.). Oliver (1951) described and named the unit. The semicerioid to phaceloid *Heliophyllum halli joshuense* n. subsp. is associated with solitary *H. halli halli* in the Joshua. It is Givetian in age.

6. *Darien.*—The Darien coral bed is in the upper part of the Wanakah Shale Member of the Ludlowville Formation in western New York. The nature and extent of the bed is discussed by Brett *et al.* (1983, p. 84–85). The *Heliophyllum*-rich part of the bed is in a limited area of Genesee County, centering around Darien (Alexander Quad.), where it is approximately 0.3 m thick. It is Givetian in age.

7. *Jaycox (Greens Landing).*—A prominent coral bed in the lower part of the Jaycox Member of the Ludlowville Formation was described and discussed as the Greens Landing coral bed by Mayer *et al.* (1994). Specimens of *Heliophyllum* are common at many localities from eastern Erie County (Buffalo Creek, East Aurora Quad.) to Canandaigua Lake (Greens Landing, Canandaigua Lake Quad., Ontario Co.), a distance of over 100 km. According to Mayer *et al.*, the bed has a maximum thickness of 1 m. The astreoid *H. halli confluens* Hall is apparently limited to this bed where it is associated with numerous *Heliophyllum halli halli.* It is Givetian in age.

8. *Deep Run.*—The Deep Run population occurs in the lower 0.5 to 2 m thick interval of the Deep Run Shale Member of the Moscow Formation at many localities from eastern Erie County to the east side of Seneca Lake (Seneca Co.), a distance of 140 km. This is not a coral bed, rather, occurrences are sporadic; solitary and weakly phaceloid *H. halli halli* (Wells', 1937, "form *praecoquus*") are associated with colonies of the phaceloid *H. delicatum* Oliver and Sorauf and diverse other shelly invertebrates. For description of the general stratigraphy see Baird (1979) and Brett and Baird (1994). The extent and occurrence of the *Heliophyllum* fauna are described in Oliver and Sorauf (1994). The Deep Run is Givetian in age.

9. *Fall Brook.*—The Fall Brook coral bed is in the Windom Shale Member of the Moscow Formation; it was described and named by Baird and Brett (1983) and discussed several times later (*e.g.*, Brett and Baird, 1994). The bed is 0.5 to 2 m thick; parts with large corals (including *Heliophyllum*) are mostly in the Genesee Valley, near Leicester and Geneseo (Livingston Co.). Our population is from the Little Beards Creek locality, just north of Leicester; this is also a possible source for the species neotype (see Systematic Paleontology section). The coral bed is in the Middle *varcus* Zone, of Givetian age.

10. *Bellona.*—The Bellona coral bed is in the Tully Limestone which immediately overlies the Hamilton Group over much of the state. The Tully and the coral bed were described in great detail by Heckel (1973). The bed has a maximum thickness of 8 cm, but has a west to east extent of over 100 km. Large solitary corals, including *Heliophyllum halli halli* and the astreoid *H. halli bellonense* n. subsp., span much of this distance. Our collections are from just west of Seneca Lake (Stanley Quad., Yates Co.) to Skaneateles Lake (Spafford Quad., Cayuga Co.), a distance of 60 km. The Bellona bed is in the Middle *varcus* conodont Zone, of Givetian age. The *Heliophyllum* specimens are the youngest known in New York, and possibly the youngest anywhere.

## AGE OF THE HAMILTON GROUP

Kirchgasser (2000) reviewed available information on the positions of Devonian stage boundaries in eastern North America and the following notes are based on his discussion. Most of the stage assignments in the Hamilton Group are derived from the conodont work of G. Klapper, summarized in Klapper (1981) and in Text-figure 1.

The Hamilton Group and Tully Limestone are Mid-

dle Devonian in age. Centerfield and younger populations (populations 3–10) are well dated within the Lower and Middle *varcus* conodont Zones and by definition are Givetian. The next older well-dated stratigraphic unit is the Cherry Valley Limestone within the *kockelianus* Zone in the upper Eifelian (Text-fig. 1). The Cherry Valley is below populations 1 and 2 leaving both as either late Eifelian or early Givetian in age. Klapper (1981, p. 61) suggested that the Mottville and higher members of the Skaneateles Formation could logically be assigned to the *ensensis* Zone on the basis of available conodont data. This would make our Case Hill population (2) early Givetian. Some workers have placed the base of the Givetian as low as the top of the Cherry Valley Limestone or within the overlying Chittenango Shale (see summary discussion of Kirchgasser, 2000); either boundary would be below our Halihan Hill population (1).

We conclude that the Halihan Hill and Case Hill populations (1, 2) are more likely early Givetian in age than late Eifelian, although the older one is very close to the boundary. The Centerfield and higher populations (3–10) are Givetian.

## BIOGEOGRAPHY

The Early and Middle Devonian world was remarkably provincial and corals were among the most provincial of marine animals (Oliver, 1977, 1980, 1990; Oliver and Pedder, 1989). Three marine biogeographic realms are recognized: 1) the Eastern Americas Realm (EAR) included the North American Plate east of the Transcontinental Arch and south of the central Canadian Shield, and northern South America (with principal coral faunas in Venezuela and Colombia); 2) the Old World Realm (OWR) was much larger, including most of the rest of the world's rich coral faunas; and 3) the Malvinokaffric Realm included areas that were at a high Devonian southern latitude; the realm was coral poor, presumably because of cold water.

Three Middle Devonian EAR provinces are recognized (Text-fig. 3): 1) the Appohimchi Province was the Appalachian-Ouachita belt (including New York and neighboring areas); 2) the Illinois-Iowa-Michigan Basins-Hudson Platform Province included areas north of the Ozark and Nashville Domes and west of the Cincinnati, Findlay and Algonquin Arches; and 3) the Venezuelan-Colombian Province (with the typical EAR *Heliophyllum* fauna; Wells, 1943; Scrutton, 1973; Oliver, 1989a, p. 3–4). All of the *Heliophyllum* described in this paper are from the Appohimchi Province, but previously described specimens from Venezuela are noted in the synonymies and the Illinois and Michigan Basin faunas are discussed.

Text-figure 3.—Devonian paleogeography shown on a modern outline map of North America showing generalized plate boundaries and biogeographic divisions. North America east of the Transcontinental Arch was part of the Eastern Americas Realm (EAR), divided into the Appohimchi Province (Appalachian Belt or Basin) and the Illinois-Iowa-Michigan Basins-Hudson Platform Province (I, Io, M, and HP on map). Most of the *Heliophyllum* spp. described or cited in this paper are from New York (just below the B in Belt). Modified from Oliver and Pedder (1989, fig. 2).

## ENVIRONMENTS AND PALEOECOLOGY

Among the generally large, dissepimented rugose corals in the Hamilton Group, specimens of the *Heliophyllum halli* species group are second in abundance only to co-occuring specimens of cystimorphs (*Cystiphylloides* and *Zonophyllum* spp.) Their abundance and wide distribution indicate that members of the complex of species and subspecies were well adapted to life on and in fine clastic sediments. The nature of this adaptation is indicated partly by corallum form and partly by inference based on preservation details and character of the enclosing rocks. Most coralla are unbroken but many are abraded, commonly on the upper side as preserved in the rock. This, and the abundance of epibionts (*Aulopora* spp., bryozoans, and less common echinoderm holdfasts; Baird and Brett, 1983, fig. 5) on the coral exteriors in some situations, indicate long exposure on the sea floor.

*Depositional environments.*—In the Hamilton Group, *Heliophyllum* spp. lived in the well-oxygenated

shallow shelf environments where gray, somewhat calcareous muds were deposited (Brett *et al.*, 1983); the coral beds described in the stratigraphy section are found within this facies along with other shallow-marine fossil assemblages that include corals in association with other animals. Environmental interpretations are based on the type of sediment and sedimentary features as well as on taphonomic features and the morphology of the preserved skeletons. For *Heliophyllum* spp., as for corals generally, larval settlement was the most vulnerable stage of life. For most corals, a hard substrate was optimal; this could be a hard ground or an accumulation of shelly material to which larvae could attach. The Staghorn Point coral bed was built on and is coextensive with a siltstone platform that provided a surface on which initial growth was feasible (Oliver, 1951). In contrast, the Joshua coral bed was initiated by the development of a 30 cm thick layer of a branching colonial rugosan, *Eridophyllum,* which could successfully spread over the mud surface and form a hard platform of another sort (Oliver, 1951). Other apparently suitable substrates were areas of hardened mud or shell accumulation (Baird and Brett, 1983, p. 426). On these varied surfaces of quite different origins, larval settlement and attachment took place. *Heliophyllum* and other corals were adapted to grow by cementing to available materials with talons, or by being laterally supported by sediment or larger fragments of shells or other corals.

Away from areas of suitable substrate, the muds appear to have been extremely soft and easily disturbed by storms or currents, resulting in turbid water over water-saturated muds. Larvae would be easily smothered in such situations but, given a start, large corals could grow partly buried in and supported by the sediment. Such a substrate would be unstable and frequent toppling of corals could be expected; but, even without water movements, increased skeletal mass with growth would produce instability and toppling. Bioturbation may also have been a factor in causing instability. Baird and Brett (1983, p. 433) suggested that bioturbation was the principal cause of toppling; we think that physical factors were more important, but more detailed study in the field is needed to determine if any cause predominated and what other factors may have been involved.

*Adaptations.*—The Hamilton *Heliophyllum* and associated corals appear to have been adapted to living in turbid waters. In living corals, life in turbid waters is facilitated by having large numbers of tentacles and a ciliated, mucus-secreting ectoderm. According to Hubbard and Pocock (1972) silt-sized or finer particles can be removed by cilia and by entanglement in mucus that is then sloughed off; larger particles can be removed by controlled distention (swelling) of the polyp and by tentacular action. *Heliophyllum* polyps probably had some of these abilities. The large numbers of septa in *H. halli* suggest equally numerous tentacles, possibly in two rings corresponding to the major and minor septa (Fedorowski, 1997). Polyp distention with arching of the oral surface may have been facilitated by the septal carinae that would have increased the polyp's "grip" on its base. Analogy with living corals described by Yonge (1940) suggests that the reflexed peripheral platform of many coralla would also have helped the sediment-shedding operation.

Corallum shape is, at least partly, an ecological adaptation. Shape variation is discussed in another section but some forms are clearly related to life in turbid conditions. Patellate, almost platelike form indicates rapid increase in diameter relative to height; it provides a relatively flat base that would resist overturning. Patellate *Heliophyllum* commonly have reflexed peripheral platforms and may have depended on distension and ciliary action to resist burial in the mud. Polyps of long, straight individuals, if supported in an erect position, would have been above much of the mud that would be in motion near the mud-water interface. Some elongate individuals are found in this growth position (*e.g.,* Brett and Baird, 1986, fig. 1). In elongate coralla, geniculations (right-angle bends) are common and indicate toppling; apparently recovery was rapid and recorded in the skeleton by widely spaced tabulae and the presence of large dissepiments on the convex side of the bend (Sorauf, 2001).

Talons are well developed in many solitary *Heliophyllum.* These are rootlike extensions of the lower dissepimentarium that provided attachment to a hard substrate. Talons near the apex of some specimens reflect the shape of the hard object such as a shell, pelmatozoan stalk, or another coral, that may have been alive or lying on the sea-bottom. Talon development in some specimens continued to a diameter of 3 or 4 cm, possibly permitting a rough estimate of the maximum size of coral that could be supported by such attachment (Sorauf, 2001).

Rejuvenation results from rapid diameter decrease during the growth of skeleton and polyp, followed by expansion. The decrease may indicate polyp trauma due to muds encroaching on the calice margin. The continued formation of outer wall and epitheca through the episode of diameter decrease protected the polyp from the mud and permitted the continued growth and rejuvenation.

*Summary.*—The abundance of *Heliophyllum* individuals in the gray shale facies of the Hamilton Group indicates that they were well adapted to life in a turbid water environment. Most, however, are found in coral

beds or in widespread calcareous units. The coral beds formed on relatively hard surfaces of greater or lesser extent; the Centerfield was a widespread shale and limestone unit with an abundant and varied shelly fauna. The Bellona (Tully Limestone) environment seems to have been a little of each kind; the coral bed rests on a relatively firm base in a widespread limestone (Heckel, 1973). Not all Hamilton *Heliophyllum* are preserved in such favorable situations. Some did live in the muds, either apparently isolated or in assemblages that were too scattered to be recognized as a coral bed or other named unit. The Deep Run population is of this type; specimens of *H. halli* and *H. delicatum* are widespread over a distance of 140 km, but no locality produced more than a few of either species. They were clearly opportunistic; larvae seem to have been there to occupy local hard attachment sites when they became available.

## PREVIOUS SYSTEMATIC WORK

Previous work on *Heliophyllum* from areas within the Eastern Americas Realm, including Venezuela, is noted and discussed in Systematic Paleontology. However, "*Heliophyllum*" and "*H. halli*" have been listed and described from many additional parts of the world, warranting separate discussion. Most of these non-EAR reports are unconvincing or unacceptable, either because of inadequate information or because the specimen(s) on which the report is based lack characters that we consider diagnostic. In 1988 we reviewed reported occurrences and summarized what seemed acceptable at that time (Oliver and Sorauf, 1988, p. 4–5, table 1). We are more sceptical now. The genus and probably the species occur in northwest Africa (LeMaitre, 1947; Coen-Aubert, 1987; Pedder, 1999) and Spain (Oliver and Sorauf, 1988) but reported occurrences in other areas, especially Asia, now seem more questionable, most of them because they are based on inadequate samples. A major purpose of this paper is to demonstrate the need for population studies of species as variable as *H. halli*. We hope that our descriptions and illustrations will provide a better basis for comparison than has been available previously. Our synonymies are intended to be reasonably comprehensive for the Eastern Americas Realm only; Old World Realm materials are included only if particularly pertinent.

*H. halli* is one of the most common rugose corals in the Middle Devonian of eastern North America. Most specimens are solitary but, in New York, four stratigraphically limited populations of colonial *Heliophyllum* differ from each other, but are intimately associated with solitary forms and are clearly closely related. This close relationship, represented by the inclusion of solitary and colonial forms in the same species, has long been accepted by some paleontologists who have worked on New York *Heliophyllum*. Most important, because of included discussions, are Nicholson (1876, p. 245, 246), Wells (1937), Sorauf and Oliver (1976), and Oliver (1989b, 1997a). In contrast Hall (1877), Fenton and Fenton (1938), Ehlers and Stumm (1953), and Coen-Aubert (1987) interpreted solitary and colonial forms (except weakly fasciculate ones) as separate species. We recognize three of the colonial populations as subspecies and the fourth as a species in the *H. halli* species group.

Table 1.—Abbreviations used in descriptions and in Tables 2 and 3.

| |
|---|
| A. Characters measured or counted in thin sections (Table 2). |
| d, corallite diameter |
| $d^t$, tabularium diameter |
| n, number of major septa |
| w, width of dissepimentarium ($d-d^t/2$) |
| c, number of carinae on major septa |
| r, corallite radius (½ d) |
| l, length of major septa |
| $l^m$, length of minor septa |
| tab, number of tabulae per cm |
| N, sample size (number of specimens or populations) |
| B. Ratios (dimensionless numbers used to reduce or eliminate the effect of size) |
| $d^t/d$ (relative width of tabularium) |
| n/d (septal ratio; higher ratios indicate more closely spaced septa) |
| c/w (approximates the number of carinae per mm) |
| l/r (length of major septa relative to corallite radius) |
| $l^m/w$ (length of minors relative to width of dissepimentarium). |
| C. Exterior measurements (Table 3); other features: |
| D, maximum diameter |
| L, length (measured along the convex side of the bent or curved corallum). |
| C, cardinal septum |
| K, counter septum |

## MORPHOLOGY AND INDIVIDUAL VARIATION IN *HELIOPHYLLUM HALLI*

*Terminology.*—Most morphologic terms are used here as defined in the 1956 *Treatise* (Moore *et al.*, 1956). Additional terms or usages are explained here, in Table 1, or in the systematic descriptions. All descriptions, except of form and external features, are based on thin sections.

Existing terminology for description of trabeculae is inadequate, perhaps indicating that pattern variation is too great for easy classification. The revised *Treatise* (Hill, 1981, p. F14) illustrates simple monacanthine and two types of compound trabeculae, rhabdacanthine and rhipidacanthine, based on the studies of Hill (1936) and Jell (1969) of two different rugose coral families. The compound forms bear only a partial similarity to the *Heliophyllum* trabeculae described as Types II and III by Sorauf and Oliver (1976).

*Carinae.*—Carinae are flangelike elevations on the sides of septa. They are fundamental parts of the septa and have the same or comparable microstructure. Parts of septa between carinae are termed intercarinae. *Heliophyllum* septa are trabeculate and carinate. Each carina is formed by one or more simple or compound trabeculae; the intercarinae consist of several parallel, simple elements that may or may not be fine trabeculae. Within each septum, carinae and intercarinae grew as a unit, but at any growth position, the carinae projected above or inward from the intercarinae forming a denticulate septal margin. Growth lines on septa mark the positions of the distal edge of septa during growth; these and the carinae indicate growth direction and shape of the calice. Carinae are perpendicular to growth lines; in the outermost dissepimentarium they are approximately parallel to the wall but lean outward in specimens with a reflexed calicinal platform. In the inner dissepimentarium they bend toward the axis and may be nearly horizontal at the tabularium margin. Carinae are commonly limited to the dissepimentarium but are present in the tabularium of some individuals.

In transverse sections, carinae are described as yard-arm, zigzag, irregular, or complex. In *Heliophyllum,* yard-arm carinae are the most characteristic but combinations of yard-arm and one or more of the other kinds in a single section are common.

Sorauf and Oliver (1976) described three types of carinae in Hamilton *Heliophyllum.* Type I carinae were defined as formed by a single monacanthine trabecula. Type II were formed by compound trabeculae prolifically branching at high angles. Type III were composed of subparallel, bundled trabeculae with infrequent branching at a low angle. In working with much larger samples for this monograph, we have recognized and used the same classification but we note more variation and less clear boundaries between the types and more extensive descriptions are given in the following paragraphs.

Type I carinae are formed by single monacanths consisting of an axis and radiating fibers of calcite; the fibers are at a constant angle to the axis, diverging in the direction of growth, and giving a featherlike appearance to the trabeculae in longitudinal sections. Sorauf and Oliver (1976, p. 339–340) noted that this is the characteristic type of carina in early growth stages of *Heliophyllum halli* and we have found no exceptions to this generality in the additional material studied.

Type I carinae are also common in later, more mature stages of many individuals (*e.g.,* Pl. 3). With growth, the monacanths may thicken and become bushy in appearance. With further growth, or with better preservation or resolution, some of these become rhabdacanth-like with second-order trabeculae seeming to take the place of the fibers. They differ from rhabdacanths in that the second-order trabeculae are longer in the septal plane than at right angles to it, giving an elliptical cross-section to the trabecula; "typical" rhabdacanths are equidimensional in cross-section. Some carinae are rhipidacanth-like with the second-order trabeculae radiating from a point or a succession of points. In longitudinal sections through trabecular axes, the second-order trabeculae have diameters of 0.08 to 0.16 mm. Vepreculae seen (as stiples) in longitudinal sections tangential to the first-order trabeculae, are the axes of the second-order trabeculae cut transversely. These compound trabeculae are referred to Type IIb (*e.g.,* Pl. 8), to differentiate them from Type IIa discussed in the next paragraph. Carinae showing the progression from Type I to IIb are designated Type I→IIb. With growth and increased corallite diameter, Type I and Type IIb trabeculae tend to fan out in the mid-plane of the septum, and new trabeculae are inserted midway between the older ones. Occasional low-angle branching of Type I or IIb trabeculae has been noted; this is one kind of Type III. In transverse sections, most Type I carinae are yard-arm; the bushy or more complex derivatives of Type I are irregular.

Type II (now Type IIa; *e.g.,* Pl. 7) carinae, as originally defined, are rhipidacanth-like but with branching primarily in the plane of the septum. They consist of a succession of fans (bushes) of second-order trabeculae branching or radiating from points. They are similar to our Type IIb but larger. Second-order trabeculae of our original Type II examples (Sorauf and Oliver, 1976, pl. 3, figs. 2–4) have diameters of 0.20 to 0.40 mm, more than twice the size of those noted above for Type IIb. However, diameters of the first-order trabeculae of Types IIa and IIb both range from 1.0 to 1.5 mm (in the plane of the septa) and there are second-order trabeculae of intermediate sizes. Both are Type II but the size range is notable. In transverse sections of *Heliophyllum,* Type II carinae are zigzag to irregular.

Type III carinae (*e.g.,* Pls. 4, 17) are the most complex type seen. Some appear to be braided with two or three strands (first-order trabeculae?) seeming to interweave; smaller branches (second-order trabeculae?) are irregularly spaced (some with intervening open spaces) and at irregular angles to the main strands. The carinae as a whole may branch at low angles. In transverse sections of carinae, these are the most complex in appearance. Type III trabeculae develop from Type I and are designated as Type I→III where this is evident in longitudinal sections.

Confirmation of carina type requires a longitudinal

thin section, but good guesses can be made from transverse sections in many instances. Well-developed yard-arm carinae, especially if attenuate, are almost always Type I. Zigzag carinae are commonly Type I or II. Irregular and complex carinae tend to be Types II and III, respectively, but they are difficult to separate in transverse sections.

*Gross internal morphology.*—Variation in morphologic features that can conveniently be measured or counted is summarized in Table 2. Some characters that are difficult to analyze quantitatively are discussed here; these include discontinuous septa, relative thickness of major and minor septa, and the complexities of dissepimental structures between septa. These could have been analyzed on a presence-absence basis but there is so much variation in each character, from slight to extreme, that this was deemed impractical.

In transverse sections of presumably mature parts of the *Heliophyllum* skeleton, major and minor septa can be: 1) equal in thickness (*e.g.,* Pl. 2), or major septa can be up to twice as thick as the minors (*e.g.,* Pl. 5); 2) complete (*e.g.,* Pl. 10), or minors, and less frequently majors, can be discontinuous, commonly in the outer dissepimentarium (*e.g.,* Pl. 3); and 3) separated (or connected) by simple, discrete, gently curved dissepiments (*e.g.,* Pl. 2), or a network of lateral and irregular transverse dissepiments can dominate the interseptal spaces (*e.g.,* Pl. 5).

In *Heliophyllum halli,* these characters vary within individuals (even in a single transverse section) and populations. There are some correlations; uniformly attenuate septa tend to be complete peripherally and to be separated by simple dissepiments, but thick major/thin minor septa are commonly associated with peripheral discontinuities and complex dissepimental networks. In addition, attenuate septa commonly have Type I carinae, but bushy Type I and Types II and III carinae tend to occur in thicker septa. Some individuals more or less conform to these combinations of characters but, in most populations and in the species as a whole, the three characters vary independently and all combinations are found. Attenuate septa can be discontinuous with or without a network and septa can be uniformly thickened and have any type of carinae.

*Growth form; solitary/colonial.*—Variation in the external form of Hamilton *Heliophyllum halli* is extreme (see, *e.g.,* Pls. 1 and 16) ranging from low turbinate to elongate ceratoid or cylindrical, from smooth to very irregular, and from solitary to astreoid. Interpretation of this variation in Hamilton *H. halli* has a long and controversial history. Nicholson (1876) included various solitary and colonial forms in his concept of the species at the same time that Hall (1877) was illustrating and naming five new species (two colonial) and two new varieties (subspecies) from Hamilton collections, largely on the basis of form.

Wells (1937) studied large new collections and recognized "intermediate stages" between Hall's species and varieties. He concluded that only one species was represented but divided *H. halli* into one "variety" (subspecies) and 11 "formae" that were the result of continuous individual variation. At the same time, Fenton and Fenton (1938) described and illustrated seven species (two new) and four subspecies (one new) from the New York Hamilton, mostly from the Hall collection.

In large collections, the boundaries between the nominal species and subspecies of Hall and of Fenton and Fenton disappear; there are too many intermediate forms. In addition, we have found no internal characters that correlate with form and would support separation. We agree with Wells' broad interpretation and consider that most of the Hall (1877) and Fenton and Fenton (1938) taxa are *H. halli.* We have recently discussed these questions in both colonial (Oliver, 1997a) and solitary (Sorauf, 2001) forms and consider that only the branching *H. delicatum* Oliver and Sorauf (1994) and the small *H. cribellum* n. sp. can reasonably be recognized as separate species.

*Ontogenetic variation.*—Most *Heliophyllum halli* individuals followed a pattern of continuing diameter increase throughout their lives whether solitary or within a colony. In solitary forms, the septa are commonly dilated in an early stage, even completely filling the lumen. These two characteristics make the recognition of the conventional ontogenetic stages impractical in most individuals. With growth, dilation may become restricted to the axial region, and eventually eliminated. Partial dilation may persist in the axial region or along the full length of the septa to a greater or lesser extent. Transverse sections of the early, completely dilated stage of large individuals, or of small individuals with fully dilated septa, are difficult to interpret. Septa can be recognized but carinae may be obscure. Most coralla with complete early stage dilation begin to open up at a diameter of approximately 20 mm. We have arbitrarily set this as a working boundary between immature and mature. Our statistical samples include data from sections with diameters 20 mm or more unless exceptions are noted. It is important to emphasize that using data from "mature" stages only does not eliminate ontogeny as a factor in our analyses of variation. The corals continued to grow and expand and only a few reached a steady state morphology. Environmentally controlled diameter decrease in mature corals and subsequent rejuvenation,

Table 2.—Character data for species, subspecies, and populations described in text. Within each box the upper figure is the mean value of the character indicated at the top of the column, and the lower figure is the observed range of values for that character. The data are arranged in stratigraphic order; numerals and names in the left column are those assigned to the 10 populations of *Heliophyllum halli halli*. Data for the four colonial subspecies and species are entered immediately below the data for the associated population. The summary data near the bottom of the chart are based on the population means for populations 2 to 10; population 1 data are excluded as explained in the text. The *H. cribellum* data at the bottom are unrelated to the rest of the table but this placement facilitates comparison.

| Population | d | $d^t$ | $d^t/d$ | n | n/d | w | c | c/w | l | l/r | $l^m$ | $l^m/w$ | tab | N | Carinae type | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | | Dominant | Secondary |
| 10–Bellona | 30.4 | 12.5 | 0.42 | 35.6 | 1.21 | 8.8 | 6.6 | 0.77 | 14.8 | 0.99 | 8.2 | 0.94 | 15.4 | 25 | I bushy | III, IIb |
| | 20/40 | 8/17 | 0.33/0.54 | 27/44 | 0.95/1.58 | 5.5/12.5 | 4/11 | 0.44/1.09 | 10/20 | 0.92/1.03 | 5/12 | 0.75/1.08 | 11/21 | | | |
| *bellonense* | 26.1 | 7.4 | 0.29 | 26.3 | 1.02 | 9.4 | 20.0 | 2.03 | 12.9 | 0.98 | 9.4 | 1.01 | | 7 | III | I |
| | 20/30 | 6/10 | 0.23/0.35 | 22/31 | 0.85/1.21 | 6.5/11.5 | 15/26 | 1.58/2.40 | 10/15 | 0.88/1.08 | 7/11 | 0.96/1.08 | | | | |
| 9–Fall Brook | 38.8 | 16.8 | 0.44 | 38.0 | 1.02 | 11.0 | 9.1 | 0.87 | 18.9 | 0.98 | 10.3 | 0.95 | 15.1 | 20 | I | III |
| | 24/57 | 10/26 | 0.32/0.58 | 31/45 | 0.61/1.54 | 5.0/18.5 | 5/13 | 0.49/1.22 | 12/28 | 0.83/1.03 | 5/16 | 0.62/1.08 | 11/30 | | | |
| 8–Deep Run | 35.1 | 14.6 | 0.42 | 39.3 | 1.14 | 10.2 | 9.8 | 0.97 | 16.2 | 0.92 | 10.1 | 0.98 | 15.4 | 18 | I to IIb | I, III |
| | 27/46 | 10/20 | 0.24/0.54 | 30/50 | 0.78/1.48 | 7.0/17.0 | 6/20 | 0.64/1.55 | 12/22 | 0.81/1.00 | 6/17 | 0.75/1.05 | 9/25 | | | |
| *delicatum* | 31.3 | 11.0 | 0.35 | 31.3 | 1.01 | 10.2 | 11.6 | 1.16 | 14.6 | 0.93 | 9.8 | 0.97 | 16.2 | 31 | Ia | III |
| | 21/42 | 8/14 | 0.24/0.45 | 25/40 | 0.71/1.32 | 6.0/14.0 | 6/18 | 0.57/1.63 | 9/19 | 0.67/1.04 | 6/14 | 0.77/1.14 | 11/23 | | | |
| 7–Jaycox | 38.2 | 13.6 | 0.36 | 36.5 | 0.99 | 12.3 | 14.6 | 1.20 | 18.3 | 0.96 | 12.1 | 1.00 | 15.7 | 26 | I | III (IIb rare) |
| | 19/54 | 8/19 | 0.26/0.52 | 25/48 | 0.69/1.32 | 5.5/18.0 | 4/25 | 0.44/2.10 | 10/27 | 0.78/1.05 | 6/18 | 0.86/1.08 | 11/28 | | | |
| *confluens* | 34.4 | 11.1 | 0.33 | 31.8 | 0.93 | 11.7 | 19.5 | 1.69 | 16.8 | 0.96 | 11.7 | 1.01 | 16.4 | 16 | III | I |
| | 25/47 | 8/16 | 0.21/0.41 | 26/37 | 0.66/1.15 | 7.5/18.5 | 12/29 | 1.15/2.42 | 13/22 | 0.85/1.06 | 8/16 | 0.81/1.16 | 11/26 | | | |
| 6–Darien | 30.2 | 10.0 | 0.33 | 36.7 | 1.20 | 10.2 | 7.9 | 0.79 | 13.9 | 0.92 | 7.5 | 0.74 | 17.0 | 13 | II | I |
| | 23/36 | 8/12 | 0.28/0.40 | 34/40 | 1.03/1.48 | 7.0/12.0 | 6/10 | 0.67/1.00 | 11/17 | 0.80/1.00 | 5/11 | 0.48/0.92 | 11/27 | | | |
| 5–Joshua | 40.3 | 16.0 | 0.41 | 45.2 | 1.16 | 12.0 | 12.4 | 1.09 | 19.4 | 0.97 | 11.8 | 1.00 | 16.7 | 25 | I bushy | III |
| | 25/52 | 12/21 | 0.23/0.57 | 36/54 | 0.81/1.60 | 5.5/20.0 | 4/22 | 0.60/2.22 | 13/26 | 0.87/1.04 | 5/19 | 0.75/1.56 | 10/26 | | | |
| *joshuense* | 35.4 | 14.0 | 0.39 | 42.7 | 1.24 | 10.7 | 17.8 | 1.75 | 16.7 | 0.97 | 10.4 | 1.00 | | 18 | III | IIb |
| | 20/55 | 9/24 | 0.17/0.54 | 33/54 | 0.84/1.70 | 5.0/17.5 | 10/25 | 1.20/3.00 | 10/27 | 0.85/1.00 | 5/17 | 0.88/1.26 | | | | |
| 4–Staghorn Pt. | 31.3 | 12.8 | 0.44 | 39.1 | 1.27 | 9.2 | 8.4 | 0.92 | 13.3 | 0.85 | 7.7 | 0.84 | 16.4 | 12 | I | III, IIb? |
| | 22/40 | 8/17 | 0.32/0.57 | 32/48 | 1.06/1.58 | 6.0/13.5 | 5/18 | 0.57/1.33 | 9/18 | 0.72/1.00 | 5/12 | 0.65/1.08 | 12/22 | | | |
| 3–Centerfield | 31.3 | 13.8 | 0.45 | 35.8 | 1.19 | 8.7 | 6.4 | 0.77 | 14.9 | 0.94 | 8.0 | 0.92 | 13.6 | 24 | I bushy | IIb |
| *–A* | 22/42(64) | 9/20(23) | 0.30/0.73 | 31/41(52) | 0.81/1.79 | 3.5/20.5 | 4/11 | 0.54/1.23 | 9/21(32) | 0.69/1.00 | 4/13(21) | 0.71/1.20 | 5/22 | | | |
| | 25.1 | 10.7 | 0.43 | 36.4 | 1.49 | 7.2 | 7.3 | 1.04 | 11.6 | 0.94 | 7.1 | 0.98 | 15.8 | 20 | I | IIb |
| *–B* | 18/37 | 8/14 | 0.35/0.52 | 30/44 | 1.03/1.85 | 5.0/12.0 | 5/11 | 0.71/1.60 | 8/19 | 0.82/1.03 | 4/11 | 0.88/1.06 | 12/20 | | | |
| | 28.5 | 12.4 | 0.44 | 36.1 | 1.33 | 8.0 | 6.8 | 0.89 | 13.4 | 0.94 | 7.6 | 0.95 | 14.7 | 44 | I to | IIb |
| total | 18/42(64) | 8/20(23) | 0.30/0.73 | 30/44(52) | 0.81/1.85 | 3.5/20.5 | 4/11 | 0.54/1.60 | 8/21(32) | 0.69/1.03 | 4/13(21) | 0.71/1.20 | 5/22 | | I bushy | |
| 2–Case Hill | 33.2 | 13.4 | 0.41 | 38.7 | 1.19 | 9.9 | 6.6 | 0.66 | 15.4 | 0.93 | 8.4 | 0.85 | 17.3 | 21 | I | III rare |
| | 25/41 | 10/16 | 0.32/0.50 | 34/43 | 0.89/1.72 | 6.5/14.0 | 4/15 | 0.47/1.25 | 10/20 | 0.73/1.00 | 5/12 | 0.59/1.08 | 12/22 | | | |
| 1*–Halihan | 20.3 | 10.2 | 0.51 | 34.1 | 1.71 | 5.0 | 4.6 | 0.93 | 9.9 | 0.98 | 4.9 | 1.01 | 19.2 | 15 | I | bushy rare |
| Hill | 15/25 | 9/12 | 0.36/0.67 | 28/40 | 1.33/2.27 | 2.5/8.0 | 3/6 | 0.71/1.25 | 8/12 | 0.90/1.07 | 3/8 | 0.71/1.20 | 14/24 | | | |
| *H. halli halli* | 34.0 | 13.6 | 0.41 | 38.4 | 1.17 | 10.2 | 9.1 | 0.91 | 16.0 | 0.94 | 9.3 | 0.92 | 16.0 | 9 | I | III, II |
| by population | 28.5/40.3 | 10.0/16.8 | 0.33/0.44 | 35.6/45.2 | 0.99/1.27 | 8.0/12.3 | 6.6/14.6 | 0.66/1.23 | 13.3/19.4 | 0.85/0.99 | 7.5/12.1 | 0.74/1.00 | 14.7/17.3 | | | |
| *H. cribellum* | 14.0 | 5.8 | 0.42 | 26.4 | 1.97 | 4.1 | 7.4 | 1.86 | 5.2 | 0.73 | 3.8 | 0.95 | 17.9 | 30 | I | |
| | 10/20 | 3/8 | 0.30/0.50 | 22/34 | 1.44/2.40 | 2.5/6.0 | 4/16 | 1.33/2.67 | 3/8 | 0.56/0.91 | 2.5/6.0 | 0.70/1.33 | 11/24 | | | |

already discussed, are additional complications (Sorauf, 2001).

Not all *H. halli* fit this generalized ontogenetic pattern. Many solitary *H. halli* have little early stage dilation, but we used the arbitrary cut-off, regardless. In addition, few individuals in colonies show early stage dilation; in most instances, we do not know whether or not their protocorallites did.

In addition to the characteristic early-stage septal dilation, all immature-stage carinae and trabeculae are yard-arm and Type I but, as noted in the discussion of carinae, this condition persisted in early "mature" stages and throughout the lives of many larger individuals.

## SYSTEMATIC PALEONTOLOGY

### Introduction

Our taxonomic unit terminology follows Oliver (1997a, p. 54–55). Descriptions are partly based on samples that we term *populations.* These are assemblages of *individuals* from a limited stratigraphic interval and geographic area that one would recognize as representing a species-level taxon if no other information were available. For this purpose a colony is an individual. Each population is assumed to include several coral generations and embraces much individual variation. Ten populations of solitary corals and four of colonies, from 10 different stratigraphic units or intervals (Text-fig. 1), were statistically analyzed to determine the amount and nature of any differences within and between populations.

If sufficiently distinct, populations may be recognized as *species* or *subspecies,* depending on degree of distinctness and other circumstances. Both are morphologically defined; *species* are separated from other species by recognizable morphologic gaps. Our goal is to recognize species that are analogous to those of living corals; these are commonly based on morphology also (see Veron, 1995, p. 229). *Subspecies* are morphologically separable populations or groups of populations within species (Mayr, 1970, p. 210). Presumably they are potential species although our subspecies are based on unique morphologies that represent one end of a continuum connecting them to another subspecies (of the same species). See Oliver (1997a, pp. 54–55) for more extensive discussion.

Our *species group* is a cluster of species more similar, and presumably more closely related, to each other than to other species of *Heliophyllum.*

Localities are in New York State unless otherwise indicated; map quadrangles (Quads.) belong to the USGS 7.5 minute series.

### Repositories

This study of *Heliophyllum* is based primarily on collections made by one or both authors over a period of 50 years; a few specimens have been contributed by other individuals. The collection data for this material are recorded in the U.S. Geological Survey, Silurian-Devonian catalog (USGS-SD numbers); all specimens from these collections that are illustrated, or individually cited in any other way, are deposited in the U.S. National Museum of Natural History (USNM). Specimens from older USNM collections and from other museums have served taxonomic purposes or been used to illustrate certain points. The following abbreviations are used in the text:

AMNH—American Museum of Natural History, New York, N.Y.
FMNH—Field Museum of Natural History, Chicago, Illinois.
NYSM—New York State Museum, Albany, N.Y.
OCGM—Oberlin College Geological Museum, Oberlin, Ohio.
OSU—Orton Museum, Ohio State University, Columbus, Ohio.
MNHN—Muséum National d'Histoire Naturelle, Paris, France.
PRI—Paleontological Research Institution, Ithaca, N.Y.
USGS—U.S. Geological Survey, Washington, DC.
USNM—U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC.

### Systematics

Phylum **CNIDARIA** Hatschek, 1888

Class **ANTHOZOA** Ehrenberg, 1834

Subclass **ZOANTHARIA** de Blainville, 1830

Order **RUGOSA** Milne-Edwards and Haime, 1850

Family **ZAPHRENTIDAE**
Milne-Edwards and Haime, 1850

Genus **HELIOPHYLLUM** Hall *in* Dana, 1846a

*Cyathophyllum* (*Heliophyllum*) Hall *in* Dana, 1846a, p. 356; 1846b, p. 183; Dana, 1849, pl. 26, fig. 3 (?), (not fig. 4).

*Cyathophyllum* Goldfuss. Rominger, 1876, p. 98–99 (in part); Lambe, 1901, p. 133–134 (in part). Not Goldfuss, 1826.

*Heliophyllum* Hall. Milne-Edwards and Haime, 1850, p. lxix; 1851, p. 408; Billings, 1859, p. 124; Nicholson, 1874a, p. 24–25 (in part); 1874b, p. 58–59 (in part); 1875, p. 141–143 (in part); 1878, p. 44–51 (in part); Nicholson and Thompson, 1877, p. 149–150; Holmes, 1887, p. 15 (in part); Grabau, 1899b, p. 124; Fenton and Fenton, 1938, p. 209–210; Stewart, 1938, p. 35–36 (in part); Lang, Smith, and Thomas, 1940, p. 66; Smith, 1945, p. 25; LeMaitre, 1947, p. 30 (in part); Stumm, 1949, p. 21; Wang, 1950, p. 217 (in part); Hill, 1956, p. F278; Cranswick and Fritz, 1958,

p. 36; Stumm and Tyler, 1962, p. 267; Scrutton, 1973, p. 256–257; Oliver, 1974, p. 174; 1976, p. 123–124; Sorauf and Oliver, 1976, p. 331–343; Hill, 1981, p. F296; Coen-Aubert, 1987, p. 154; Oliver and Sorauf, 1988, p. 5; Pedder, 1990, p. 91–92; Oliver and Sorauf, 1994, p. 1185, 1188; Pedder, 1999, p. 405.

*Heliophyllum* Dana. Sloss, 1939, p. 58.

*Heliogonium* Chapman, 1893, p. 45; Stumm, 1949, p. 21; Hill, 1956, p. F278; 1981, p. F296; Pedder, 1990, p. 91.

*Heliophylloides* Stumm, 1949, p. 18; Hill, 1956, p. F278; 1981, p. F296; Pedder, 1990, p. 91.

*Hexagonaria* Gürich. Stumm, 1948b, p. 11–13 (in part). Not Gürich, 1896.

*Billingsastraea* Grabau. Stumm, 1949, p. 35 (in part); Ehlers and Stumm, 1951, p. 85 (in part); 1953, p. 9 (in part); Stumm, 1955, card 230 (in part). Not Grabau, 1917.

*Type species.*—*Heliophyllum halli* Milne-Edwards and Haime, 1850, as replacement name for *Strombodes helianthoides*? Hall, 1843, p. 209–210, text-fig. 87-3 (pl. 48, fig. 3 is same figure). Not *Strombodes helianthoides* of Phillips, 1841, or *Cyathophyllum helianthoides* Goldfuss, 1826, to both of which Hall, 1843 referred. Middle Devonian (Givetian), Hamilton Group, New York.

*Date of publication.*—Confusion regarding the date(s) of publication of Dana's "Zoophytes" was removed by Stumm (1948a) who presented evidence that the official text of volume 7, printed by C. Sherman, Philadelphia, was published in 1846 (as indicated on the title page), not 1848 as stated by Lang *et al.* (1940, p. 173). Parts of the text describing fossil corals were excerpted the same year in the *American Journal of Science*. The plate volume was published in 1849. We cite these as Dana 1846a, 1846b, and 1849, respectively.

*Diagnosis.*—Solitary and colonial rugose corals, widely varying in corallum form and size, characteristically having moderately deep calice with broad flat, inclined, or reflexed peripheral platform and shallow cardinal fossula. Major septa commonly long and bilaterally arranged about cardinal-counter plane; mature septa generally attenuate but commonly dilated in early ontogenetic stages, especially in solitary forms. Carinae abundant and very prominent, commonly long or short yard-arm, but zigzag carinae are also present and may predominate; carinae generally limited to dissepimentarium. Septal trabeculae simple or compound, commonly both. Dissepiments globose in numerous rows. Tabulae incomplete or complete. (Modified from Oliver and Sorauf, 1994, p. 1185.)

*Discussion.*—*Heliophyllum* is one of the most common rugose corals in the Middle Devonian of the Eastern Americas Realm. In New York, specimens, mostly *H. halli,* are present to abundant in upper Emsian (Bois Blanc Formation) to upper Givetian (Tully Limestone) strata (Text-fig. 1); this is our principal area and range of study. *H. halli* and other species have been described or noted in rocks within the same age range from Venezuela to the Hudson Bay Lowlands and from many localities in the Illinois, Michigan, and Appalachian Basins (Text-fig. 3). Most of the many nominal species from the Illinois and Michigan Basins need further study before their status can be evaluated.

Rominger (1876), Hall (1882, 1883, 1884), Davis (1887), Greene (1898–1906), and others named hundreds of Emsian to Givetian "species" of rugose corals from the Falls of the Ohio River area in and around Louisville, Kentucky, in the southeastern part of the Illinois Basin. Stumm (1965) reviewed and outlined the history of Falls work and provided yeoman service in locating and putting on record type specimen data, reillustrating many of the types, and synonymizing some two-thirds of the "species." Still, with few exceptions, species descriptions are based only on the external morphology of silicified specimens and most *Heliophyllum* species from the Falls area are identifiable only at the generic level. Stumm (1965) referred most solitary *Heliophyllum,* and some branching ones, to this genus, but astreoid and cerioid forms were referred to *Billingsastraea* and *Hexagonaria,* respectively.

A second important source of nominal *Heliophyllum* spp. is the Traverse Group (Givetian) in Michigan. This group is of particular interest because it represents facies comparable to the age-equivalent Hamilton Group of New York. Solitary *Heliophyllum* are common; they were most recently revised by Stumm and Tyler (1962) who described nine species and subspecies including *H. halli.* All of the taxa need restudy to determine the extent of individual variation and whether or not some are synonyms. *Billingsastraea romingeri* (Ehlers and Stumm, 1951) is a probable Traverse colonial *Heliophyllum.* This and other Traverse "*Billingsastraea*" need restudy, but there is no indication that any are conspecific with any of the solitary forms.

Most *Heliophyllum* are solitary, but dendroid, phaceloid, cerioid, and astreoid colonies are known. Most of the colonial forms seem to be distinct species; Oliver (1976, pp. 123–133) described several from the Bois Blanc and Onondaga Formations (Emsian and Eifelian) in New York and Southwestern Ontario, and additional species are known from Emsian to Givetian-age rocks in many other parts of the EAR. As far as we know, *H. halli* is unique among *Heliophyllum* spp. in that it includes both solitary and colonial forms.

Our principal concern in this paper is to describe, classify, and interpret typical *Heliophyllum halli* and allied forms from the Hamilton Group in New York. Our taxonomic framework is as follows:

*Heliophyllum halli* species group

*H. halli* Milne-Edwards & Haime, 1850
*H. halli halli* Milne-Edwards and Haime, 1850
Form "*praecoquus*" of Wells, 1937
*H. halli confluens* (Hall), 1877
*H. halli bellonense* new subsp.
*H. halli joshuense* new subsp.
*H. delicatum* Oliver & Sorauf, 1994
*H. stewarti* Oliver & Sorauf, 1994
*H. cribellum* new species

### HELIOPHYLLUM HALLI species group

*Diagnosis.*—Species of *Heliophyllum* with characters in common that suggest that they are more closely related to *H. halli* and each other than to other species of the genus.

**Heliophyllum halli** Milne-Edwards and Haime, 1850

*Type specimens.*—Holotype by monotypy, the specimen illustrated by Hall (1843, fig. 10, p. 209) is now lost or mislaid. Neotype, MNHN IP S.11661, illustrated by Milne-Edwards and Haime (1851, pl. 7, figs. 6, 6a, 6b), designated by Coen-Aubert (1987, p. 155, pl. 1, figs. 1, 2), who prepared and illustrated thin sections; reillustrated herein, Plate 10, figures 1 and 2.

*Occurrence of neotype.*—Milne-Edwards and Haime (1851) did not indicate the source of their illustrated specimen but Coen-Aubert (1987) indicated that the following information accompanies the specimen: Hamilton Group, Moscow (now Leicester), Livingston County, New York. This would almost certainly be the Windom Shale Member, Moscow Formation, Givetian, and probably the Fall Brook coral bed (our population 9). The appearance of the specimen is compatible with this source.

*Diagnosis.*—Solitary, branching, cerioid and astreoid *Heliophyllum*; solitary forms and corallites in colonies range up to 6 cm or more in diameter. Calice with axial pit, small, well-marked cardinal fossula, and with or without a peripheral platform. Major septa commonly long and biradially arranged; minor septa limited to wide dissepimentarium within which septal carinae are abundant on both major and minor septa. Tabularium typically occupies approximately one-third the diameter; tabulae incomplete or complete. Septal and carinal trabeculae are simple or branching monacanths and/or compound with varying complexities.

*Outline history.*—Detailed synonymies accompany the descriptions of the subspecies and related species. The following annotated chronology outlines the nomenclatural and interpretational history of *Heliophyllum halli*:

1843. *Strombodes helianthoides*? Hall, p. 209–210, fig. 87-3 (pl. 48, fig. 3 is same); (not Goldfuss, 1826, or Phillips, 1841). Hall's illustrated specimen became holotype by monotypy in 1850; specimen now lost or mislaid.

1850. *Heliophyllum halli* Milne-Edwards and Haime, p. lxix. Based species on Hall (1843), making Hall's single illustrated specimen the holotype.

1851. *H. halli* Milne-Edwards and Haime. Milne-Edwards and Haime, p. 408–409, pl. 7, figs. 6, 6a, 6b. First illustrations after Hall's (1843) woodblock print; this single illustrated specimen was designated neotype by Coen-Aubert (1987).

1876. *H. halli* Milne-Edwards and Haime. Nicholson, p. 245. Early discussion of variation within the species.

1877. *H. halli* Milne-Edwards and Haime and new species. Hall, pls. 23–27. Illustrations of *H. halli* and seven new species and "varieties" gives relatively complete representation of form variation in *H. halli* as we understand it; see subspecies synonymies for details.

1937. *H. halli* Milne-Edwards and Haime. Wells, p. 5–20. First modern analysis of individual form variation in this species. Wells' formae have no standing in formal taxonomy but are included in synonymies for clarity and completeness.

1938. *Heliophyllum* spp. of Milne-Edwards and Haime, Hall, and new species. Fenton and Fenton, p. 211–227, figs. 1–19, pl. 17–22. Followed Hall (1877), in recognizing many species that we consider synonyms of *H. halli*.

1976. *H. halli* Milne-Edwards and Haime. Sorauf and Oliver, p. 331–343, pl. 1–5. Described, illustrated and discussed microstructural variation in this species.

1987. *H. halli* Milne-Edwards and Haime. Coen-Aubert, p. 151–162, pl. 1–5. Detailed description of "typical" form; essentially restricted species to solitary forms with simple trabeculae; selected original of Milne-Edwards and Haime (1851, pl. 7, fig. 6, 6a, 6b) as neotype.

1997a. *H. halli* Milne-Edwards and Haime. Oliver, p. 55–60, pl. 1–2. Discussed varied relationships of colonial and solitary forms.

2001. *H. halli* Milne-Edwards and Haime. Sorauf, p. 24–33, figs. 3–5. Detailed analysis and interpretation of shape variation in solitary forms.

### Heliophyllum halli halli
Milne-Edwards and Haime, 1850
Plates 1–13

*Strombodes helianthodes*? Hall, 1843, p. 209–210, text-fig. 87-3 (pl. 48, fig. 3 is same fig.). Not Goldfuss, 1826 or Phillips, 1841.

*Cyathophyllum* (*Strombodes*?) *turbinatum*? Hall, 1843, pl. 49, fig. 1, (?). Not Goldfuss, 1826.

Subgenus *Heliophyllum*. Dana, 1849, pl. 26, fig. 3, (?) (not fig. 4).

*Heliophyllum halli* Milne-Edwards and Haime, 1850, p. lxix; 1851, p. 408–409, pl. 7, figs. 6, 6a, 6b; 1853, p. 235–236, pl. 51, fig. 3 (part?); Hall, 1859, p. 89–90, (part?); Billings, 1859, p. 126; Nicholson, 1874a, p. 26–27, fig. 4, (part?).
*Cyathophyllum hallii* (*sic*) Milne-Edwards. Rominger, 1876, p. 99–101, pl. 35, upper tier, 4 specimens left and center, (?).
*H. halli* Milne-Edwards and Haime. Hall, 1877, pl. 23, figs. 1–5, 12, pl. 25, figs. 1–7.
*H. halli* var. *reflexum* Hall, 1877, pl. 23, figs. 6–11.
*H. irregulare* Hall, 1877, pl. 24, figs. 1–7, 13.
*H. arachne* Hall, 1877, pl. 24, figs. 8–12, 14.
*H. degener* Hall, 1877, pl. 25, figs. 8–11.
*H. halli*? var. *obconicum* Hall, 1877, pl. 25, figs. 12–13.
*H. proliferum*? Hall, 1877, pl. 26, fig. 5.
*H. halli* Milne-Edwards and Haime. Nicholson, 1878, figs. A, B (p. 46); Hall, 1883, p. 259, pl. 6, fig. 1, (?); 1884, pl. 16, figs. 4–5, (?).
*Cyathophyllum halli*. Davis, 1887, pls. 77, 92, figs. 2, 3, (not?).
*H. halli* Milne-Edwards and Haime. Holmes, 1887, p. 15, pl. 3, fig. 2, a-e; Grabau, 1899a, p. 124–125, fig. 7.
*Cyathophyllum halli* Milne-Edwards and Haime. Lambe, 1901, p. 148–150 (in part).
*H. halli* Milne-Edwards and Haime. Brown, 1909, p. 75–78, figs. 21a–f; Cleland, 1911, p. 28–29, pl. 1, fig. 5, (?).
*Cyathophyllum halli* Milne-Edwards and Haime. Branson, 1924, p. 49–50, text-fig. $2_{1-4}$, pl. 1, fig. 1, (?).
*H. halli* Milne-Edwards and Haime. Stewart, 1927, p. 19, pl. 1, fig. 3, (?).
*H. halli* forma *typicum* Wells, 1937, p. 9–10, 18, pl. 1, figs. 1–4, text-figs. 1–7.
*H. halli* forma *praecoquus* Wells, 1937, p. 11, 18, pl. 1, figs. 5–6, 12, text-figs. 10–11.
*H. halli* forma *reflexum* Hall. Wells, 1937, p. 11, text-figs. 12–14.
*H. halli* forma *irregulare* Hall. Wells, 1937, p. 11, 15, 18.
*H. halli* forma *pravum* Wells, 1937, p. 11, 18, pl. 1, figs. 13–15, text-figs. 15–16.
*H. halli* forma *arachne* Hall. Wells, 1937, p. 14, 18, pl. 1, fig. 7, text-figs. 17–19.
*H. halli* forma *degener* Hall. Wells, 1937, p. 14, 18, text-fig. 20.
*H. halli* forma *obconicum* Hall. Wells, 1937, p. 14, 18, text-fig. 21.
*H. halli* forma *aplatum* Wells, 1937, p. 18, pl. 1, figs 10–11, text-fig. 30.
*H. halli* forma *infundibulum* Wells, 1937, p. 18, pl. 1, figs. 8–9, text-fig. 29.
*H. halli* Milne-Edwards and Haime. Fenton and Fenton, 1938, p. 211–214, pl. 17, figs. 1–5, pl. 18, fig. 1, text-fig. 6.
*H. halli degener* Hall. Fenton and Fenton, 1938, p. 214–215, pl. 17, figs. 6–8, pl. 18, fig. 2.
*H. halli irregulare* Hall. Fenton and Fenton, 1938, p. 215–216, pl. 18, figs. 3–6, text-fig. 8.
*H. decorosum* Fenton and Fenton, 1938, p. 216–217, pl. 18, figs. 7–9, text-fig. 5.
*H. arachne* Hall. Fenton and Fenton, 1938, p. 217, 219, pl. 17, figs. 1–2, text figs. 1–2.
*H. obconicum* Hall. Fenton and Fenton, 1938, pl. 19, figs. 1–5, pl. 20, figs. 8–10, text-figs. 9–10.
*H. obconicum* form *confluens* Hall. Fenton and Fenton, 1938, text-figs. 14–19 (part?), not pl. 21, fig. 1.
*H. obconicum teres* Fenton and Fenton, 1938, p. 222–223, pl. 19, fig. 6, pl. 20, figs. 1–7, pl. 21, fig. 3, text-figs. 11–13.
*H. reflexum* (Hall). Fenton and Fenton, 1938, p. 224–225, pl. 22, figs. 4–5, pl. 23, fig. 1, text-figs. 3–4.
*H.*? *asperum* Fenton and Fenton, 1938, p. 225–226, pl. 21, figs. 4–6, text-fig. 7 (?).
*H. halli* Milne-Edwards and Haime. Stewart, 1938, p. 37–38, pl. 6, figs. 7–8, (?); Stumm, 1942, pl. 82, fig. 11, (?); Wells, 1943, p. 363–364 (95–96), pl. 36 (10), figs. 1–2; Smith, 1945, p. 26, pl. 33, figs. 3a–b; Le Maitre, 1947, p. 34–35, pls. 1, 2, 3, fig. 1, (?).
*H. halli* var. *nodulosa* Le Maitre, 1947, p. 34–35, pl. 3, figs. 4–6, (?).
*H. halli* Milne-Edwards and Haime. Stumm, 1949, p. 21, pl. 9, figs. 8–11, not? fig. 12; Wang, 1950, pl. 6, fig. 40; Lecompte, 1952, p. 475, fig. 118a–c; Hill, 1956, p. F278, fig. 190-4a, b; Ma, 1956, p. 48, pl. 41, figs. 1a–b, pl. 42, fig. 1, pl. 57, figs. 1–9, pl. 58, figs. 1–6 (in part); Cranswick and Fritz, 1958, p. 36–37.
*H. halli* var. *dilatiseptatum* Cranswick and Fritz, 1958, p. 37–38, pl. 1, fig. 5, (?).
*H. halli* Milne-Edwards and Haime. Stumm and Tyler, 1962, p. 268–269, pl. 1, figs. 15–16, pl. 2, figs. 7–8, (?).
*H. halli bellense* Stumm and Tyler, 1962, p. 269, pl. 1, figs. 6–7, pl. 2, figs. 3–4, (?).
*H. halli potterense* Stumm and Tyler, 1962, p. 269–270, pl. 1, figs. 4–5, pl. 3, figs. 10–13, (?).
*H. halli* Milne-Edwards and Haime. Kato, 1963, text-fig. 12(10–13), (?); Stumm, 1965, p. 36, pl. 32, figs. 5, 6, 20–23 (in part); Stumm, 1968, p. 38, pl. 1, figs. 1–2, pl. 3, fig. 13.
*H. halli* forma *praecoquus* Wells. Stumm, 1968, p. 38 (not). = *H. stewarti* Oliver and Sorauf, 1994. Not Wells, 1937.
*H. halli* Milne-Edwards and Haime. Stumm, 1968, p. 38, pl. 1, figs. 1–2, pl. 13, fig. 13; Oliver, 1971, p. 196, pl. 3, figs. 1, 7, 9; Scrutton, 1973, p. 257–260, pl. 5, figs. 6–8, pl. 6, figs. 1–6; Sorauf and Oliver, 1976, p. 331–343 (part, solitary forms only).
*H. halli halli* Milne-Edwards and Haime. Coen-Aubert, 1987, p. 155–162, pls. 1–5.
*H.* sp. cf. *H. halli* Milne-Edwards and Haime. Oliver and Sorauf, 1988, p. 9, figs. 4A–F, (?).
*H. halli halli* Milne-Edwards and Haime. Pedder, 1990, pl. 4.1, figs. 1–11; Oliver, 1997a, p. 56 (including form "*praecoquus*" of Wells), pl. 1, figs. 1–4, 7.
*H. halli* Milne-Edwards and Haime. Sorauf, 2001, p. 24–33, 3 pls. (figs. 3–5).

*Type specimens.*—Same as for species.

*Diagnosis.*—*H. halli* that are solitary or with small, short (commonly <2 cm) offsets, rarely forming dendroid colonies of several corallites.

*Discussion.*—It is convenient to refer solitary *H. halli*, and small semicolonial forms that seem to be parts of solitary populations, to *H. halli* subspecies *halli*. Wells (1937) used the name *H. halli* forma *typicum* in such a restricted way that it is not suitable for this purpose; Wells clearly meant "*typicum*" to refer to the form's generalized shape, central to the *H. halli* complex, without systematic implications. In any case, as noted by Oliver (1997a) and below, Wells' formae have no standing in formal nomenclature. As far as we know, Coen-Aubert (1987) was the first to use the trinomial *H. halli halli* in formal recognition of the typical subspecies, although her concept was more restricted than ours. Specimens of *H. halli halli* are in coral beds and elsewhere in the gray, calcareous shale facies of the Hamilton Group. In the overlying Tully Limestone, they are limited to the Bellona coral bed.

Table 3.—Maximum known size of *Heliophyllum halli halli* specimens in each stratigraphic unit represented by an analyzed population. The column headings are explained at the bottom of the table; measurements are in mm and cm as indicated

| Population | d | ORd | D | H |
|---|---|---|---|---|
| 1. Halihan Hill[1] | 20.3 mm | 15/25 mm | 3 ½ cm | 8 cm |
| 2. Case Hill | 33.2 mm | 25/41 mm | 4 cm | 11 cm |
| 3. Centerfield | 28.5 mm | 18/64 mm | 6 cm | 16 cm |
| 4. Staghorn Point[2] | 31.3 mm | 31/40 mm | 5 ½ cm | 7 ½ cm |
| 5. Joshua[3] | 40.3 mm | 25/52 mm | 6 cm | 12 cm |
| 6. Darien | 30.2 mm | 23/36 mm | 6 cm | 11 cm |
| 7. Jaycox | 38.2 mm | 19/54 mm | 6 cm | 18 cm |
| 8. Deep Run | 35.1 mm | 27/46 mm | 5 cm | 15 cm |
| 9. Fall Brook | 38.8 mm | 24/57 mm | 6 cm | 14 cm |
| 10. Bellona | 30.4 mm | 20/40 mm | 4 cm | 14 cm |

d, ORd—Mean and Observed Range of diameter in thin sections; in mm (from Table 2.) D, H—Maximum diameter and height (length measured on specimen's convex side) in largest and longest specimen; in cm.

[1] See text discussion of small size in this population.

[2] Hall (1877, pl. 25) illustrated a specimen with height of approximately 10 cm.

[3] Wells (1937) reported maximum diameter and height of 6.5 and 14 cm respectively.

The offsetting forms are scattered through the section and nowhere form a recognizable population.

*Terminology.*—Table 1 gives abbreviations for skeletal characters measured or counted in thin sections (Table 2) and hand specimens (Table 3) and explains our use of ratios in analyses of thin section data.

Additional terms used to describe morphology as it appears in transverse sections are from our discussion of "Morphology and Individual Variation": *network* and *simple* refer to the most and least complex dissepimental structures between septa; *continuous* and *discontinuous* refer to peripheral parts of the septa, usually the minors; *equal* and *thick and thin* refer to the relative thickness of the major and minor septa, usually in the outer dissepimentarium.

*External features.*—Neglecting irregularities, form varies from turbinate to cylindrical with trochoid and ceratoid coralla being most common. Rare individuals expanded at an apparently steady rate but growth is irregular in most with erratic expansions and contractions of the outer wall; the corallum is smoothly or irregularly curved, or geniculate (Sorauf, 2001), rarely straight. Maximum size varies within and between populations (Table 3) but ranges up to diameters of 6 to 6.5 cm and heights of 16 to 18 cm in the Centerfield and Jaycox. Wells (1937) reported diameters up to 8 cm and lengths of 22.5 cm in Hamilton specimens from various (unspecified) New York localities. Small individuals are common but it is impractical to recognize a lower limit to observed ranges of size because diameter increase continued through the life of most individuals.

Calices are bowl shaped, moderately deep with a well marked cardinal fossula. Calice walls commonly slope gently upward to a broad, flat or reflexed peripheral platform or, less commonly, to the outer wall. Upper edges of septa serrated by projecting, rounded ends of carinae. Calice floor flat, slightly depressed, or gently arched.

External markings are fine growth lines and coarser growth increments as well as longitudinal septal grooves and interseptal ridges. The finer growth lines and septal grooves are present on unworn exteriors, but the epitheca is commonly worn without preservation of detail. However, in some individuals the fine growth lines are so well preserved as to provide evidence of individual age as demonstrated by Wells (1963). Wells' pioneering work on annual growth was based on New York Hamilton corals. He suggested an age of approximately 13 years for one specimen (10 cm in height) and a duration of approximately 400 days for the Devonian year.

*Internal features.*—Measurements and counts of various skeletal elements are given in Table 2. Means and observed ranges aid in comparing populations but are primarily of use in demonstrating overlap between populations and the overall range of variation in Hamilton specimens of *H. halli halli.* All of the characters tabulated are more or less size dependent and to some extent controlled by extrinsic factors (*e.g.*, age at death and environment of growth). The ratios are dimensionless and more useful than means and observed ranges for comparing individual and population differences.

Major septa are long; commonly some extend to or nearly to the corallite axis while others are shorter. Minor septa are generally restricted to the dissepimentarium. Septa biradially arranged; in the calice the C is marked by a fossula; in transverse sections below the calice, the C-K plane is commonly marked by a short C and long K, but the K varies and may be short or the same as other major septa; if short, the C-K plane is evident but the two protosepta may not be separable unless the K is flanked by long minor septa. Carinae are present to abundant on both major and minor septa in the dissepimentarium.

Septal thickness and continuity in transverse sections varies both ontogenetically and within mature individuals and populations; this is described in the section on Morphology and Individual Variation.

Tabularia occupy one-third to nearly one-half of the corallum diameter leaving over half the space in longitudinal sections to numerous rows of dissepiments (Table 2). The dissepiments vary in size and shape, at least partly depending on position on the convex or concave side of a bent or geniculate corallum (Sorauf,

2001). In longitudinal sections, there is no apparent difference between the simple and network dissepimentaria noted in transverse sections. Tabulae are complete or incomplete; the former are flat or somewhat depressed near the axis with downturned margins; incomplete tabulae or tabellae tend to form an arched pattern. There are gradations between the two extremes and both can occur in the same specimen. Whether they are complete or incomplete is determined by the amount of open space in the axial region; numerous shorter or more attenuate septa tend to correlate with more numerous complete tabulae, whereas a preponderance of major septa extending to the axis leaves space only for incomplete tabulae or tabellae.

*Microstructure.*—The wall is two-layered; an inner, light-colored layer is thicker, and apparently composed of fibers radially arranged in transverse sections, inclined upward in longitudinal sections. The outer layer, epitheca, is thin, darker and of less certain fine structure.

The trabecular microstructure of the septa and the abundant carinae is described in the section on Morphology and Individual Variation.

*Increase.*—Wells (1937) based two of his formae on offsetting at different stages. One of these, "forma *praecoquus,*" is interpreted as a variant of *H. halli halli.* Form "*praecoquus*" has one to four or more peripheral offsets. Protocorallites are commonly small, but diameters up to 4.5 cm are known; offsets tend to be short (1–2 cm). Specimens are not common but have been found in several of our populations and elsewhere in the Hamilton, associated with other solitary and colonial *Heliophyllum.* The three specimens illustrated by Wells (1937, pl. 1, figs. 5, 6, 12, text-figs. 10, 11) are from the Staghorn Point population; the specimen of Oliver (1997a, pl. 1, figs. 1, 2) is from the Jaycox population. Additional specimens in our collections are from the Centerfield, Staghorn Point, Darien, Jaycox, and Deep Run populations. Specimens from the Staghorn Point and Jaycox populations are illustrated on Plates 12 and 13. In the lower Deep Run Shale, "*praecoquus*" occurs with the branching *H. proliferum,* which differs in the long tapering form of its corallites and common increase by lateral offsetting (see description below).

Wells described *H. halli* forma *praecoquus* as having "precocious buds," that is, offsets developed at an early stage. This variant is interesting for its incipient coloniality. Wells' (1937) other offsetting form, "forma *proliferum,*" has a distinct morphology, includes large colonies, and occurs as a stratigraphically limited population that we recognize as a species (*H. delicatum* Oliver and Sorauf, 1994; see below). Wells clearly differentiated between *formae* and *varieties* in describing individual variation in *H. halli* (Wells, 1937). Under the current code of zoological nomenclature, his variety is a subspecies but his formae have no standing. However, "*praecoquus*" has been cited in the literature and we include it in our synonymy, even though we do not accord it formal recognition.

*Population analyses.*—In each of the 10 populations analyzed statistically, most of the measured specimens are individuals for which at least two thin sections, transverse and longitudinal, have been prepared. Additional sections, especially transverse ones, are available for many of these, but tabulated data are from the highest section, most commonly one from just below the base of the calice. Insofar as was practical, data from immature individuals, or early stages of apparently mature ones, are not included in the tabulations but sections of these and of other excluded specimens (poorly or incompletely preserved, single section, etc.) provided additional information for descriptions. Photographs on Plates 2 to 11 are grouped by population. They illustrate variation in the subspecies but do not adequately show variation in the individual populations which, in some, is as great as in the subspecies as a whole.

1. *Halihan Hill population.*—The analyzed sample (Table 2) includes 15 specimens from the Halihan Hill coral bed in eastern New York. Only seven or eight of these would have been used in the analysis of any of the other populations because specimens are small, mostly immature individuals (in Table 2 note size characters and that these data are not used in the subspecies totals). Early stage septal dilation masks other characters, but comparable early stage individuals from other populations show some mature characters, so the Halihan Hill data is of value for some comparisons. In addition, these are the oldest Hamilton *Heliophyllum* and should be included for the sake of completeness. Morphologically, the population is the simplest of the 10 analyzed (see Pl. 2, figs. 8–13). Septa are peripherally attenuate with only rare discontinuities or lateral dissepiments. Long and short yard-arm carinae are most common, zigzag carinae are uncommon. Almost all carinae are Type I, some are moderately bushy; Type I→III were seen in only one or two individuals.

Thirteen of our specimens came from a locality just west of Mount Marion (Ulster County), two specimens are from the Helderberg area (Albany County). Lane (1955) noted that the Halihan Hill corals were smaller than those from other coral beds. A later collection from Ver Straeten's (1994) roadcut locality near Kingston (Ulster County) includes a few *H. halli halli* with diameters at the base of the calice up to 3.5 cm (Table

3) but these were collected too late to be included in the Table 2 analysis.

2. *Case Hill population.*—The total sample includes 37 thin sectioned individuals from the Case Hill coral bed, Mottville Member, Skaneateles Formation, at two localities on Bare Mountain, Onondaga County; 21 of these are included in the sample analyzed (Table 2). Specimen diameters are small to medium; numbers of carinae on major septa and in proportion to the width of the dissepimentarium are low; in these values the Case Hill population is comparable to the Centerfield, Staghorn Point, and Bellona populations.

Major septa are bilaterally arranged, extend somewhat over 0.9 the distance to the axis, and have relatively few carinae (Table 2). Most of the carinae are Type I (some bushy) and a few are Type I→III. In transverse sections, most interseptal space is filled by networks of lateral and small globose dissepiments intersecting at odd angles, but some are occupied by simple, discrete, gently curved dissepiments. Most septa are attenuate and complete but some thickening of major septa is seen and a few are irregularly discontinuous in the outer dissepimentarium; in earlier stages dissepiments are simple. In a few thin sections zigzag carinae are nearly as common as yard-arm; this seems to correlate with septal thickening and development of Type III trabeculae. See Plate 2, figures 1–7 for examples.

3. *Centerfield population.*—Our sample consists of over 200 sectioned individuals; 44 of these were measured and analyzed (Table 2). The Centerfield population is the most widespread of the *Heliophyllum* populations considered here; measured specimens are from localities spaced along the outcrop over an east-west distance of 120 km (75 mi). The principal localities (and counties) from west to east are: Murder Creek and East Alexander (Genesee), East of York (Livingston), Centerfield (Ontario), and Fayette (Seneca). Average specimen diameters are relatively small although they range up to 64 mm or more. Number of carinae on major septa and in proportion to the width of the tabularium are low; in these and other values, the Centerfield population is closest to the Bellona solitary population (Table 2). Major septa are bilaterally arranged and extend to or nearly to the axis.

In transverse sections, septa vary from attenuate and equal in thickness (*e.g.*, Pl. 3, figs. 9, 10) to thick and thin (major up to twice as thick as minor septa although nearly attenuate in outer dissepimentarium; *e.g.*, Pl. 3, fig. 11). In our analysis (Table 2) we separated the population into two roughly equal-sized subpopulations, A (attenuate) and B (thick and thin). These intergrade in the character used for the separation as well as in other characters (Table 2); furthermore, variation in other characters did not correlate with the A-B division. At either A-B extreme, minor septa can be peripherally complete (some or most in all specimens) or discontinuous; major septa rarely are discontinuous. Interseptal dissepiments appear simple or as a network; not uncommonly, both conditions are seen in the same individual, in either the same or successive sections. Axial dilation varies from slight to complete in immature stages and from none to significant in adults.

Type I carinae predominate, commonly bushy; Type I→IIb is present (but not common) in specimens with thicker septa, rare in attenuate forms; Type I→III was seen but is very rare.

This is our largest and most variable population. Both sample size and large source area with diverse environments are factors, but the latter is considered more important. Specimens are illustrated on Plate 3.

4. *Staghorn Point population.*—Our sectioned sample includes 29 individuals of which 12 were statistically analyzed. Collections are from three different points on Skaneateles Lake: Jenny Point, Staghorn Point, and Willow Point, representing the center and two extremities of the 2.2 km-long exposure of the coral bed; and also from the ravine at Lord's Hill (all Onondaga County). Average diameters are relatively small although large specimens are not uncommon. Major septa are bilaterally arranged (commonly with a short C), relatively short, attenuate, and commonly dilated in axial region, especially in early growth stages. Mean septal ratio is high. Minor septa are relatively short, some very short, but rarely discontinuous. Interseptal dissepiments are generally simple, but lateral dissepiments are not uncommon. A single specimen of Wells' "forma *praecoquus*" is in our sample and the three illustrated specimens of Wells (1937) are from this unit.

Type I carinae predominate, commonly bushy; Type III are uncommon; Type I→IIb are present (possibly a matter of preservation). Specimens from this population are illustrated on Plates 3 and 12.

5. *Joshua population.*—Our sectioned sample includes 31 specimens of which 25 were analyzed (data on Table 2); several specimens are illustrated on Plate 4. Collections are from two localities on Lord's Hill and four localities along Otisco Lake (all Onondaga County). Specimens are robust; major septa are long, reaching to or nearly to the axis, numerous, and bilaterally arranged. Septa are somewhat dilated, but majors are only locally thicker than minors; peripheral discontinuities are rare. Interseptal dissepiments are generally simple although lateral dissepiments are common.

Types I, I→III, and III carinae are common in ma-

ture stage; Type I carinae are thick and bushy and predominate in early stages; Type III dominates in several mature individuals; occasional bursts have Type II structure. Our "type example" of Type III carinae (Sorauf and Oliver, 1976, pl. 5, figs. 2–4; USNM 219922; herein Pl. 5, figs. 1, 2) is from this population.

The colonial, *H. halli joshuense,* occurs with this solitary population. The colonial form is similar to the solitary in many characters (Table 2 and see description). Colonial corallites are smaller and septa are proportionately more numerous. These differences are attributed to crowding in cerioid parts of the colonies and to necessarily different sampling methods. Microstructure is similar, although in the colonial subspecies Types I→III and advanced III carinae are more dominant, Type IIb is present, and there seem to be more carinae on major septa. There is considerable overlap in the observed ranges of all analyzed characters.

6. *Darien population.*—The total sample includes 18 thin sectioned individuals from the Darien coral bed, Wanakah Shale Member, Ludlowville Formation, at a single locality (Murder Creek, near Darien, Genesee County); 13 of these are included in the sample analyzed (Table 2). Specimens are medium-sized. Major septa do not reach the axis, are distinctly bilateral in arrangement, and rarely incomplete near the outer wall. Minor septa are relatively short and are commonly discontinuous peripherally; some are entirely missing in a thin section. Septa are commonly attenuate and equally thick, but majors are significantly thicker than minors in parts of some transverse sections. Interseptal dissepiments are a network in most of the sections (*e.g.,* Pl. 5, fig. 9), but one individual and parts of others are almost simple. Type IIb and I→IIb carinae (*e.g.,* Pl. 5, fig. 3) predominate and vepreculae are common; Type I occurs in immature stages of mature specimens and in small specimens that did not reach maturity (not included in analyzed lot); questionable Type III carinae were noted in three specimens. In transverse section, carinae are yard-arm, complex or zigzag, reflecting the prevalence of Types I and II.

A single individual of Wells' (1937) "forma *praecoquus*" is in the population but not in the measured sample because of its small size; the offset is peripheral, midway between the floor and margin of the calice.

Individuals in the Darien population are remarkably uniform in character. This is most likely due to the small size and limited provenance of the sample. Examples are illustrated on Plate 5.

7. *Jaycox population.*—The sample includes 53 thin sectioned individuals from the Green's Landing coral bed in the Jaycox Member of the Ludlowville Formation; 26 of the specimens are in the analyzed sample (Table 2). Approximately equal numbers of specimens are from each of three areas: 1) near the Erie-Genesee County boundary, 2) in the Genesee Valley west of York (Livingston County), and 3) both sides of Canandaigua Lake (Ontario County). Areas 1 and 3 are separated by an east-west distance of over 100 km; area 2 is approximately midway between 1 and 3. Several specimens are illustrated on Plates 6 and 7.

Specimens are robust; most have long major septa that extend to, or nearly to, the axis and are bilaterally arranged. Septa are attenuate or somewhat dilated; extra dilation in the axial area is minimal, even in early stages. Minor septa commonly nearly equal to majors in thickness; some minors short or peripherally discontinuous, but most are complete. Interseptal dissepiment structure varies from simple to network, commonly intermediate and varying within a single section.

Type I (most are bushy), I→III, and I→IIb carinae are common. Some I→IIb→III carinae suggest that Types IIb and III intergrade or are partly artifacts of preservation. Our example of Type IIa (Sorauf and Oliver, 1976, pl. 3, figs. 2–4, pl. 4, fig. 2; herein Pl. 7, figs. 1, 2) may be from this stratigraphic unit.

This population is associated with and grades into astreoid *H. halli confluens* (see description). Types I and III carinae are common in both but Type III predominates in the colonial form. Corallite diameters are comparable but mean septal number and relative number of septa are smaller and there seem to be more carinae on major septa in the colonies (Table 2). There is a large overlap between associated solitary and colonial types in the observed ranges of all of these characters.

8. *Deep Run population.*—Our sample includes 32 individuals from the lower part of the Deep Run Shale Member of the Moscow Formation; 18 specimens were statistically analyzed. Collections are from several localities in the area between East Bethany (Genesee County) and the east shore of Seneca Lake (Seneca County), a west to east distance of 100 km. Examples are illustrated on Plates 8 and 9.

Specimens are moderately robust. Major septa are long but commonly fail to reach the axis; they tend to be bilaterally arranged. Septa vary from attenuate to markedly dilated and from equal to thick and thin; axial dilation varies. Septa are commonly complete but some sections show peripherally discontinuous minors and majors and, rarely, a partially lonsdaleoid sector. Interseptal dissepiments vary from simple to complex networks, commonly more or less intermediate.

Types I (often bushy), I→IIb, and I→III carinae are

common; Types IIb and III commonly are present in the same longitudinal section. The original of text-figure 2 in Sorauf and Oliver, 1976 (renumbered USNM 498542; herein Pl. 8, figs. 1–5) is from this population at a Canandaigua Lake (Ontario County) locality.

The Deep Run solitary *H. halli halli* are associated in the field with the dendroid *Heliophyllum delicatum* Oliver and Sorauf (1994); see description. Most specimens can be assigned to species on the basis of external form; *H. halli halli* has a large apical angle and is more robust; *H. delicatum* is relatively more elongate with a smaller apical angle and mean diameter. Internally, *H. delicatum* has thinner, more delicate structures, relatively smaller tabularia, and fewer septa. See Table 2 and the description of *H. delicatum* for further comparisons.

9. *Fall Brook population.*—The sample includes 32 individuals from a single exposure of the Fall Brook coral bed, Windom Shale Member, Moscow Formation, on Little Beards Creek, north of Leicester (Livingston County); 20 of the specimens are in our statistical sample (Table 2) and several are illustrated on Plate 10.

Specimens are robust with most major septa extending to, or nearly to, the axis. Septa bilaterally arranged, attenuate to moderately thickened, commonly with long, thin cross-bar carinae. Minor septa equal to majors in thickness; some minors and rare majors are peripherally discontinuous; one specimen has additional discontinuities at the margin of the tabularium. Interseptal dissepiments vary from simple to complex networks. Axial dilation varies, commonly marked in early stages.

Type I carinae are universal in sample; most are thin in longitudinal section but some are thickened and bushy, and approach Types II or III in structure.

The neotype of *Heliophyllum halli* (MNHN IP S.11661) is probably from the Fall Brook coral bed and possibly from this locality. The general appearance and internal morphology of the neotype are compatible with this source. Six sectioned specimens from the Lansing coral bed (Tompkins County), and one from the Bay View coral bed (Erie County), both in the Windom Shale (see Text-fig. 1), have morphologies that are well within the Fall Brook population's range of variation.

10. *Bellona population.*—The sample includes 67 sectioned individuals from the Bellona coral bed in the Tully Limestone at six localities along the outcrop from Bellona (Yates County), just west of Seneca Lake to Carpenter Falls (Cayuga County), just west of Skaneateles Lake, a west to east distance of 60 km; 25 of the specimens are in the measured sample (Table 2). Illustrated specimens are on Plate 11. Two-thirds of the measured sample and three-fourths of the total sample are from Bellona.

Specimens are medium sized; major septa are long, reaching to or nearly to the axis, numerous, and are bilaterally arranged. In most transverse sections major and minor septa are equally thick, attenuate to moderately thickened, and rarely peripherally incomplete; these have relatively simple interseptal structure; a few specimens have more unequal septal thickening, more peripheral discontinuities in the minor septa, and/or a more complex dissepimental network between septa. Virtually all specimens show axial septal dilation in both immature (nearly complete) and mature stages.

In transverse sections, yard-arm carinae predominate; they are widely spaced, averaging 6–7 on major septa, a number and spacing more common in lower Hamilton populations than in upper ones (Table 2). Longitudinal sections show that most carinae are Type I (characteristically thick and bushy), but types I→IIb (*e.g.,* Pl. 11, fig. 8), and I→III (*e.g.,* Pl. 11, fig. 1) are present to common.

The Bellona solitary corals are associated with *H. halli bellonense,* an astraeoid subspecies described below. Internal structures in the two forms are quite different. The colonial form has more attenuate septa with abundant, closely spaced zigzag and yard-arm carinae (averaging 18 to 24 on major septa). The morphologic contrast between the solitary and colonial *H. halli* in the Bellona coral bed is much greater than that in the Joshua and Jaycox beds in which separation of the solitary and colonial subspecies is primarily based on growth form. See description of *H. halli bellonense* for further discussion.

*Material.*—Neotype and other illustrated specimens (Plates 1 to 13): specimen numbers and collection data (USGS catalog numbers or other information) are given in the Plate descriptions.

Other numbered specimens: Additional specimens in statistically analyzed samples, or otherwise mentioned in the text, are listed by population and collection in the Appendix.

### **Heliophyllum halli confluens** (Hall), 1877
Plates 14–19

*Cyathophyllum* (*Strombodes*?) *turbinatum*? Goldfuss. Hall, 1843, pl. 49, fig. 1 (?). Not Goldfuss, 1826.

*Heliophyllum halli.* Hall, 1859, p. 89 (?).

*Heliophyllum confluens* Hall, 1877, pl. 26, figs. 3, 4, pl. 27.

*Heliogonium* Chapman, 1893, p. 45 (part).

*Heliophyllum confluens* Hall. Grabau, 1899a, p. 126, fig. 8; 1899b, p. 288.

*H. halli* var. *confluens* (Hall). Wells, 1937, pp. 10, 14–15, 18, 19, not text-fig. 8 (see *H. halli joshuense*).

*H. obconicum* form *confluens* (Hall). Fenton and Fenton, 1938, p. 221–222, pl. 21, fig. 1 (not text-figs. 14–19).

*H. confluens* Hall. Stumm, 1942, pl. 82, fig. 16 (?).

*Heliogonium confluens* (Hall). Stumm, 1949, p. 21.
*Billingsastraea confluens* (Hall). Ehlers and Stumm, 1953, p. 8, pl. 6, fig. 4.
*B. ingens* (Davis). Ehlers and Stumm, 1953, p. 9, pl. 6, figs. 1–3 (New York material), not? pl. 5, figs. 1–5.
*B. confluens* (Hall). Stumm, 1955, cards 234, 234.1.
*B. ingens* (Davis). Stumm, 1955, card 236.1, (? cards 235, 236, 236.2); Stumm, 1968, p. 41, pl. 2, figs. 1, 2, (?).
Astreoid *Heliophyllum*, Sorauf and Oliver, 1976, p. 340–343.
*Heliogonium* or *Heliophyllum confluens* Hall. Pedder, 1990, p. 91–92.
*Heliophyllum halli* var. *confluens* (Hall). Mayer, Baird, and Brett, 1994, text-figs. 8A, B.
*H. halli confluens* (Hall). Oliver, 1997a, p. 55–56, pl. 2, fig. 1; (? pl. 1, figs. 5, 6).

*Type specimen.*—Lectotype, FMNH UC 18974, the original of Hall, 1877, pl. 27, selected by Wells, 1937, p. 10. Hall gave the locality as York, Livingston County, N.Y.; this is almost certainly the Greens Landing coral bed, Jaycox Member, Ludlowville Formation, Hamilton Group. The coral bed outcrops along Browns Creek, a mile west of York, where numerous specimens of *H. halli confluens* have been collected from both outcrop and talus.

*Comments.*—Wells (1937, p. 10) selected the original of Hall (1877, pl. 27) as "holotype" (lectotype) of *Heliophyllum halli confluens*. Stumm (1949) selected *H. confluens* as the type species of *Heliogonium* Chapman making it a subjective junior synonym of *Heliophyllum*, but his selection of the original of Hall's pl. 26, figs. 3–4 as lectotype of *H. confluens* is invalid because of Wells' (1937) earlier selection.

*Diagnosis.*—*H. halli* forming astreoid colonies consisting of from two to 40 or more corallites; both yardarm and zigzag carinae are abundant but the former predominate.

*Occurrence.*—*H. halli confluens* is known primarily from, and may be limited to, the Green's Landing coral bed in the lower part of the Jaycox Member, Ludlowville Formation, Hamilton Group, in New York. In westernmost New York, near where the Jaycox Member wedges out due to removal of higher parts, we have seen specimens in the uppermost Jaycox, directly underlying the Tichenor Limestone Member (*e.g.*, at Bullis Bridge over Buffalo Creek). Still farther west, from Lake Erie shore sections, Grabau (1899b, p. 288) reported: "This coral occurs only in the Encrinal [*i.e.*, Tichenor] limestone. Several specimens were noted in blocks of this rock on the lake shore. On Morse creek it is not uncommon in the lower Encrinal associated with the preceeding [solitary *H. halli*]."

We have not seen the Grabau material, but a large specimen in the USNM collection (USNM 133683) is labeled as from the Tichenor Limestone just southeast of Buffalo (Buffalo SE Quad., Erie County); crinoidal limestone matrix supports this provenance. Some early workers (*e.g.*, Cooper, 1930) included shaly beds below the Tichenor Limestone (of later workers) in the member; this may account for some of the Tichenor reports. Occurrences west of the Jaycox pinch-out may include lag specimens incorporated into the basal Tichenor and/or survivors into the time of Tichenor deposition; but this deposition may have begun earlier in the western area than farther east. However, some "Tichenor" occurrences are more difficult to explain. Collection locality USGS 5693-SD (Stafford Quad., Genesee County) is discussed in the Appendix as primarily a Deep Run site; however, when first visited, a *H. halli confluens* was collected "from deeply weathered Tichenor" in the roadbed, not quite in place (WAO field notes, July 1960), so the source remains questionable. For a diagram of the stratigraphic relationships see figure 2 in Oliver and Sorauf (1994); Mayer *et al.* (1994) gave a very detailed description of the Jaycox Member and Greens Landing coral bed in western New York.

Two triplets from the Prout Limestone in Ohio (Pl. 16, figs. 5–7) are similar to *H. halli confluens* but are completely silicified and cannot be confidently identified at the species or subspecies level. One of these was illustrated by Stumm (1942) and is listed in the synonymy (although queried) because of its similarity in external morphology and age.

*External features.*—Astreoid coralla are composed of 2 to 40 or more large corallites. The largest available, reasonably complete specimen is the lectotype (FMNH UC 18974): diameter, 18 by 20 cm, height (incomplete), 7.5 cm; 27 corallites are seen on the convex growing surface (Pl. 14, figs. 4, 6). The underside was covered by a holotheca, now partly worn away. Most of the corallites radiate from two central corallites, the larger of which may be the protocorallite (Pl. 14, fig. 5); the relationship of the two corallites is not clear and the possibility of the colony being a composite from the growth of two or more larvae cannot be ruled out.

Larger colonies known to us are incomplete; we estimate that some have diameters of 30 cm or more and include 40 or more corallites. The heights of some coralla more nearly equal their diameters; one such specimen is 11.5 cm high with a diameter of 18 cm (USNM 519490, "West of York," Leroy Quad., Livingston County). Smaller colonies, with fewer than 10 corallites, are more likely to be nearly complete; these most commonly have heights equal to less than half their diameters.

Corallite diameters on colony surfaces range up to more than 50 mm; commonly the larger corallites range from 30 to 40 mm. Broad, flat or gently arched peripheral platforms surround a relatively deep axial

pit that occupies the central third of the calice surface. Peripheral platforms of adjacent corallites merge, at or without a shallow depression; septa commonly are confluent, appearing to pass from one corallite to the other. Increase is lateral and/or peripheral, but offsets expand rapidly to apparently mature diameters.

*Internal features.*—A wide dissepimentarium, consisting of 10 to 20 rows of globose dissepiments, commonly occupies two-thirds or more of the corallite diameter (Table 2). The tabularium is composed of mostly incomplete tabulae that form an arched pattern with the axial ends of the long septa but, where septa are shorter, tabulae tend to be axially flat or gently concave. Many longitudinal sections show both arrangements more or less alternating.

In transverse thin sections, septa are attenuate and commonly bilaterally arranged; cardinal and/or counter septa tend to be shorter than other major septa. Major septa extend to or nearly to the axis and are more or less straight in the dissepimentarium, becoming quite irregular in the tabularium; minor septa are essentially limited to the dissepimentarium. At corallite margins, septa are confluent (thamnasterioid), or alternating in position with peripheral ends of septa that turn irregularly and form a discontinuous septal wall. Numbers of major septa range from 22 to 38 in corallite sections 20–50 mm in diameter. Carinae are abundant in the dissepimentarium, uncommon in the tabularium; most are yard-arm, but zigzag and irregular patterns are not uncommon; counts of 15 to 25 carinae per septum are typical.

*Microstructure.*—Type I→III carinae, composed of compound trabeculae branching at very low angles (see Plate 17) predominate in most corallites; type I carinae (formed by simple monacanths) are present and may predominate in parts of some individuals.

*Discussion.*—*H. halli confluens* is morphologically defined but its recognition is partly based on its distribution. It is most common in, and possibly restricted to, the Green's Landing coral bed in the lower part of the Jaycox Member. Stumm (1955 and earlier) assigned Hamilton solitary *Heliophyllum* to *H. halli*, small astreoid colonies to *Billingsastraea confluens*, and large colonies to *B. ingens* (Davis). However, in large samples there is a complete gradation in growth form from solitary to twins, triplets, etc. to colonies of 30 to 40 or more corallites. Among the associated solitary specimens, type I and III individuals also predominate; conceivably these should be considered part of the same subspecies, but other populations of solitary forms include both type I and III individuals, and many individual specimens include both type I and III carinae. Biologically, some or most of the associated solitary corals must be part of the same population and subspecies as the colonies, but it is impractical to identify them as such and the name has been applied only to compound forms.

Astreoid *Heliophyllum* of Emsian and Eifelian age in New York were described by Oliver (1976); additional astreoid taxa of Emsian to Givetian age have been named from other parts of eastern North America but most are inadequately described. All of these are known from large colonies only; they lack the essential character of *H. halli confluens*, that of forming populations of small to large colonies associated with solitary corals that appear to be conspecific.

It seems clear to us that *H. halli confluens* is too closely allied to the associated solitary corals to be a separate species. Description as a subspecies is the most satisfactory way to recognize both its special morphology and its close relationship to solitary *H. halli*.

*Material.*—Lectotype, FMNH UC 18974 (Hall, 1877, pl. 27; herein, Pls. 14 and 15, fig. 7). The lectotype and the following are illustrated but not included in the measured sample: AMNH 517241 (Hall, 1877, pl. 26, figs. 3–4), USNM 487252, 518545–518546. Specimens illustrated and included in the measured sample: USNM 518542–518544, 518548–518551; unillustrated specimens in measured sample with collection numbers: USNM 518552–518554 (USGS 5708-SD); 518555 (USGS 5693-SD); 518556–518560 (USGS 5323-SD). Cited in text as "Tichenor, SE of Buffalo", USNM 133683; cited as 11.5 by 18 cm, USNM 519490. Cited and illustrated from Prout Limestone in Ohio: OGCM 6085; USNM 518547. Collection data for illustrated specimens are given in the plate explanations; collection locality descriptions are in the Appendix.

### **Heliophyllum halli bellonense** n. subsp.
Plates 20–21

*Billingsastraea* sp. C Ehlers and Stumm, 1953, p. 10–11.
*Heliophyllum halli* form 4 ("Bellona") Oliver, 1997a, p. 56.

*Type specimens.*—Holotype, USNM 518562; Bellona coral bed, Tully Limestone, Bellona, N.Y.; collected by P. H. Heckel. Illustrated paratypes, USNM 518561, 518563–518564; unillustrated paratypes, USNM 518565–518567, 518622.

*Occurrence.*—*H. halli bellonense* is known only from the Bellona coral bed in the Tully Limestone (Givetian), west-central New York.

*Diagnosis.*—Astreoid colonies of few to many corallites; both zigzag and yard-arm carinae are present but zigzag seem to predominate, or be equal to yard-arm in numbers.

*External features.*—Exteriors of coralla poorly

known; specimens occur in massive limestone that tends to break through, rather than around the coral; coralla are partly crushed and, in addition, seem to have been eroded prior to burial; none is complete. Astreoid coralla of 3 to 10 or more corallites are known; diameters range from 5 to 20 cm; heights from 5 to 10 cm. Traces of holotheca are preserved on some specimens; no colony upper surfaces have been seen.

*Internal features.*—The dissepimentarium commonly occupies two-thirds of the corallite diameter (Table 2), and is composed of 12 to 16 or more rows of small globose dissepiments. The tabularium is composed of incomplete tabulae forming a gently arched pattern.

In transverse sections, septa are attenuate, probably bilaterally arranged but this is obscure in most corallites owing to internal crushing. Major septa extend to the axis and are more or less straight; minor septa are essentially limited to the dissepimentarium. At corallite margins, septa are confluent or irregular. The number of major septa, in corallites 20–30 mm in diameter, ranges from 22 to 31 (Table 2). Carinae are abundant in the dissepimentarium, rare in the tabularium; zigzag and yard-arm are approximately equal in number; 15 to 25 per septum were counted.

*Microstructure.*—Types I and III carinae are approximately equal in number; either type may predominate in longitudinal sections.

*Discussion.*—Description of *H. halli bellonense* is based on nine coralla from three localities in the Bellona coral bed; recognition is based on both morphology and restricted distribution. Our sample includes colonies with 3 to 10 corallites; larger colonies with more corallites are known. Few associated solitary *H. halli halli* have the internal structure of the colonies (see Table 2); most have dilated septa, widely spaced yard-arm carinae, and a relatively wide tabularium. *H. halli bellonense* is more similar to *H. halli confluens* and some of the Hamilton *H. halli halli* than it is to the Bellona solitary forms. In this clear separation from associated solitary forms, *H. halli bellonense* is unlike both *H. halli confluens* and *H. halli joshuense.*

The delicate morphology of the colonies and a few of the solitaries is more like that of Hamilton shale facies forms than that of the majority of associated solitary corals in the limestone. However, all of the Bellona *Heliophyllum* fit within the *H. halli* range of variation.

Colonies in the two astreoid populations are morphologically similar; *H. halli bellonense* seems to have greater proportions of zigzag and type I carinae than does *H. halli confluens.* Comparison is made difficult by differences in preservation and apparent abundance. *H. halli bellonense* is less well preserved and was only collected from bedding plane exposures of the limestone where there is little color difference between the coral and the matrix. In contrast, most *H. halli confluens* specimens are undistorted and occur in relatively soft shales in various kinds of outcrops where color and texture contrasts are high and collecting is relatively easy. *H. halli bellonense* may be much more common than our sample indicates. See the discussion of *H. halli confluens* for comparisons with other astreoid *Heliophyllum.*

*Material.*—Holotype, USNM 518562; illustrated paratypes, USNM 518561, 518563–518564. The measured sample includes the holotype and USNM 518563–518564 (illustrated) and the following unillustrated paratypes (with collection numbers): USNM 518565–518567 (USGS 5341-SD; Heckel, 1973, loc. 9c), and USNM 113668 ("Bellona"; *Billingsastraea* sp. C of Ehlers and Stumm, 1953). Additional paratype: USNM 518622 (USGS 8766-SD). Collection data for illustrated specimens are in the plate explanations; collection locality descriptions are in the Appendix.

**Heliophyllum halli joshuense** n. subsp.
Plates 22–28

*H. confluens* Hall. Wells, 1937, p. 10 (Lords Hill specimens only), text-fig. 8 (Type A).
*H. proliferum* Hall (not Nicholson). Wells, 1937, text-fig. 9 (? Type B).
*H. halli* form 1 ("Joshua") Oliver, 1997a, p. 55–57, pl. 2, fig. 2.

*Type specimens.*—Holotype, PRI 24560 (original of Wells, 1937, text-fig. 8); illustrated paratypes, USNM 518568–518575, 487758; unillustrated paratypes, USNM 518576–518585. All are from the Joshua coral bed.

*Occurrence.*—Known only from the Joshua coral bed, Otisco Shale Member, Ludlowville Formation, Hamilton Group in central New York. Specimens are most common at Lords Hill, 10 km SW of Nedrow, in the upper part of the coral bed; additional specimens are from a ravine on the west side of Otisco Lake; both localities are in Onondaga County.

*Diagnosis.*—Massive to fasciculate *H. halli* with discontinuous cerioid (three-layer) wall between corallites where in lateral contact.

*External features.*—Incomplete coralla are composed of 2 to 14 or more corallites. Some specimens (Type B) consist of a protocorallite and a cluster of from 5 to 13 peripheral, parricidal offsets that grow together as a massive, semicerioid colony in which individuals are separated by a discontinuous wall; protocorallite diameters up to 60 mm are known; offset diameters range from 25 to 60 mm (30–40 mm is common).

Other specimens lack a distinct protocorallite and

consist of a massive stage only (Type A); most of these seem to offset laterally although, in many cases, specimens are too incomplete to determine their growth patterns. Corallite diameters in Type A coralla range from 30 to 60 mm, and are comparable to those of Type B. All specimens referred to the subspecies have the massive, semicerioid stage in common. In general, Type A specimens have fewer corallites (2–5 or 6?) than Type B specimens (5–13, plus the protocorallite).

All specimens in our sample are worn and incomplete but corallum heights and diameters of more than 15 cm are represented. Corallites have broad, flat or gently arched peripheral platforms and a moderately deep axial pit that occupies the central third of the calice. The colony surface tends to be depressed along corallite boundaries; the wall may or may not be visable.

*Internal features.*—A wide dissepimentarium occupies one-half to two-thirds of the corallite diameter and is composed of 15 to 25 rows of globose dissepiments (Table 2). Tabulae are incomplete and form a gently arched pattern that is difficult to discern because of interference with the axial ends of the long major septa.

In transverse thin sections, septa are attenuate in the dissepimentarium and attenuate or slightly to markedly dilated in the tabularium; minor septa are limited to the dissepimentarium, commonly thinner than major septa, and locally discontinuous. Bilateral arrangement in some corallites is suggested by shorter septa that are presumed to be cardinal or counter.

Corallites are separated by a discontinuous wall that may extend for several millimeters or be virtually absent, although nearly all transverse, and many longitudinal, sections show some wall segments. Where present, the wall is a typical cerioid, three-layered wall with a dark median line and light-colored stereome on either side in which the septa are based. Where wall is lacking, septa of the adjoining corallites meet irregularly. The number of major septa, in corallite sections 25 to 50 mm in diameter, ranges from 35 to 54. Carinae are abundant in the dissepimentarium; most are yard-arm, zigzag are present but much less common; counts range from 10 to 25 per septum.

*Microstructure.*—Type III carinae are present or predominant in most sections. Type I carinae are common on minor septa and are present and may predominate locally on major septa.

*Discussion.*—*H. halli joshuense* is characterized by its fasciculate to massive growth form and internal, discontinuous, cerioid wall. We know of no other *Heliophyllum* with this combination of characters. However, recognition as a subspecies is partly based on its restricted distribution. It occurs only in the upper part of the Joshua coral bed in a very limited area. It is associated with morphologically similar solitary corals, many of which have Type III microstructure. Recognition of the subspecies boundaries pose the same problems as discussed for *H. halli confluens*; some of the co-occurring solitary corals probably belong to the same population as the colonial form, but recognition is not practical and the subspecies name is used only for the colonies.

*Material.*—Holotype, PRI 24560 (Type A, Lords Hill); illustrated paratypes, USNM 518568–518573 (Type A, Lords Hill); 518574 (Type B, Lords Hill); 518575, 487758 (Type B, Otisco Lake). Collection data for illustrated specimens are in the plate explanations. The measured sample includes the holotype and most illustrated paratypes (not 518571, 518573) and the following unillustrated paratypes, USNM 518576–518585 (all Type A, USGS 8762-SD, Lords Hill). Collection localities are described in the Appendix.

### **Heliophyllum delicatum** Oliver and Sorauf, 1994
Plate 29

*H. proliferum* Hall, 1877, pl. 26, figs. 1, 2, not fig. 5. Not Nicholson, 1874b.

*H. delicatum* Oliver and Sorauf, 1994, p. 1188–1198, figs. 3–10; Oliver, 1997, p. 56.

*Type specimens.*—Holotype, USNM 474690; 37 paratypes, USNM 474691–474727. All from the lower part of the Deep Run Shale Member, Moscow Formation, Hamilton Group, western and west-central N.Y.

*Diagnosis.*—Dendroid *Heliophyllum,* commonly offsetting laterally, forming colonies of a few to 20 or more corallites and up to 46 cm or more in diameter. Corallites ceratoid, gently expanding to diameters of 4 cm or more and with lengths of 30 cm or more. Corallites weakly constructed with thin walls, septa, and carinae, and no lateral supports. (Oliver and Sorauf, 1994, p. 1190).

*Discussion.*—For a full description and comparison with other colonial *Heliophyllum,* see Oliver and Sorauf (1994) and Oliver (1997a). All of the Hamilton colonial forms are thought to be derivatives of solitary *H. halli halli* with which they commonly occur. *H. delicatum* differs from *H. halli halli* in its long, gently tapering corallites and its delicate internal structures. Associated branching colonies of *H. halli halli* (including "form *praecoquus*") have a larger apical angle, reflecting a more rapid diameter increase relative to length, are more robust (thicker walls, septa, and carinae), and offset peripherally. Because of its distinct morphology and the lack of intermediate forms, we

interpret *H. delicatum* as a separate species, rather than a subspecies of *H. halli.*

**Heliophyllum stewarti** Oliver and Sorauf, 1994

*Heliophyllum proliferum* Nicholson. Stewart, 1938, p. 38–39, pl. 7, fig. 6. Not Nicholson, 1874a, b, or Hall, 1877.
*H. halli* forma *praecoquus*? Wells. Stumm, 1968, p. 38. Not Wells, 1937.
*H. stewarti* Oliver and Sorauf, 1994, p. 1198–1199, fig. 13, 1–7.

*Holotype.*—OSU 17732; the only known specimen. Tenmile Creek Dolomite, Middle Devonian (lower middle Givetian), south of Silica, Ohio.

*Diagnosis.*—Phaceloid *Heliophyllum,* commonly offsetting laterally, in which ceratoid corallites may remain in contact without developing a separating wall (astreoid) for several cm of linear growth.

*Discussion.*—For a full description with illustrations and comparisons, see Oliver and Sorauf (1994). *H. stewarti* differs from other known phaceloid *Heliophyllum* in having an astreoid stage. Corallites in astreoid *H. halli confluens* rarely branch but with prolonged colony growth, corallites may become laterally separated, either completely or in chains or small clusters; however, individuals remain short and none are known to develop the elongate ceratoid form of *H. stewarti.*

This brief description is included here because it adds to the overall picture of variation in EAR *Heliophyllum* and to emphasize its position in the *H. halli* species group.

**Heliophyllum cribellum** new species
Plates 30, 31

*Type specimens.*—Holotype, USNM 518586 (Pl. 30, figs. 1–8); Centerfield Member (Givetian), Ludlowville Formation near East Alexander, New York (USGS 4678-SD). Most illustrated and measured paratypes are from the same collection. See *Material* for detailed listings of paratypes from this and other localities.

*Diagnosis.*—Small, mostly ceratoid to cylindrical *Heliophyllum* with short major septa and little or no dilation in any growth stage. Relatively long and thick yard-arm carinae commonly touch those of adjacent septa giving the dissepimentarium a reticulate appearance in transverse sections.

*Comments.*—The following description is based on specimens from several Centerfield localities in the area between East Alexander (Genesee County) and Centerfield (Ontario County). The measured sample of 30 individuals (Table 2) is from a large collection at the type locality 2.9 km east of East Alexander, Genesee County (USGS 4678-SD). With minor exceptions, specimens from other localities fall within the observed ranges of variation of the measured sample.

*External features.*—Growth form is most commonly ceratoid or ceratoid→cylindrical; trochoid forms are uncommon. The cylindrical stage indicates a steady-state polyp diameter and is assumed to represent maturity; by this criterion adult diameters range from 10 to 20 mm. Specimens are small; the maximum measured diameter (in a trochoid specimen) is 22 mm; maximum observed length, more than 75 mm.

Several specimens exhibit rejuvenation. In at least one specimen, diameter contractions and expansions proceeded along a straight coral axis; in several others a 90-degree bend accompanied a more marked contraction with expansion to the former diameter in a few millimeters. Some of the latter appear to be large peripheral (and parricidal) offsets in the parental calice, but one or two specimens preserve epitheca over the pre-contraction calice that indicates rejuvenation.

Offsets, other than the questionable ones of the previous paragraph, are rare, but two specimens in the measured population have very small peripheral offsets within the calice, near the outer wall. The most notable specimen has seven offsets, each 4 to 5 mm in diameter in a calice 20 mm in diameter (Pl. 30, figs. 14–16); the second example has one or two 5 mm offsets in a 12 mm calice; another specimen from a nearby locality is similar but with three offsets. None of these offsets grew to a length of more than a few millimeters.

Calices are broad and shallow; depth is one-half the diameter or less; the sides of the calice flatten near the margin but there is no distinct peripheral platform; the distal ends of the carinae and septa project prominently on the sides. Some thin sections from just below or within the lower calice indicate the presence of a shallow cardinal fossula that is only weakly apparent in the calice itself.

Exterior markings are fine and coarse growth lines and septal grooves and interseptal ridges as in other species of the genus. Talons are present on some individuals.

*Internal features.*—Analysis of measurements and counts of various skeletal elements made from thin sections (Table 2) follow the same methods used in analyzing the populations of *H. halli* and the same definitions and qualifications apply.

Major septa are relatively short; the length of minor septa approximates the width of the dissepimentarium but commonly is more or less than that. In any transverse section, length of both major and minor septa may be quite variable. Septa are biradially arranged; the axial plane is commonly marked by shorter or longer major septa, presumably C and K; examples of long minors next to the axial plane (presumably next to K) have been seen. Some long counter(?) septa

tend discontinuously to the axis (amplexoid?) and form short vertical projections that cause tent-like upbending of one or a few tabulae; additional major septa may also extend discontinuously into the otherwise empty axial area and appear in transverse sections as detached septal fragments.

Carinae are abundant; most are yard-arm, and relatively thick; many are long enough to touch or connect with carinae extending from the adjacent septa. In transverse sections dissepimentaria look like screens or grids. This character varies in most specimens; the "screen" is locally broken by shorter yard-arm carinae and less commonly by zigzag carinae or randomly discontinuous major or minor septa. The parts of major septa that extend into the tabularium are carinate in many specimens but zigzag carinae are more common than yard-arm in this area. All observed carinae are Type I, many are bushy.

Septal dilation is minimal or absent, even in the earliest growth stages.

The tabularium occupies three-tenths to half the total diameter. Tabulae are complete, incomplete, or irregular; they are closely spaced although all counts (Table 2) are approximate. Where complete, they are axially flat and down-bent at the contact with the dissepimentarium. Some 5 to 12 rows of globose dissepiments form the dissepimentarium.

*Microstructure.*—Only simple monacanthine trabeculae (many bushy) and Type I carinae have been observed. Wall structure is as described for the genus.

*Discussion.*—The relatively short major septa and the screen- or grid-like dissepimentarium in transverse sections are characteristic and are the principal bases for the separation of *H. cribellum* from the associated *H. halli*. Lack of early stage dilation is an additional basis but this character is too inconsistent and variable in *H. halli* to be definitive.

*Distribution.*—*H. cribellum* is known only from the Centerfield Member, Ludlowville Formation, in west-central New York. Our principal sample is from near East Alexander (Genesee County) but additional specimens from the Centerfield in the outcrop belt between East Alexander and Canandaigua (Ontario County) have added to the description and known geographic range.

*Material.*—Holotype, USNM 518586, Centerfield Member, east of East Alexander (Batavia So. Quad., USGS 4678-SD). Illustrated paratypes, USNM 518587–518598; collection data is in the plate explanations. The measured sample (all USGS 4678-SD) includes the holotype and several illustrated paratypes, USNM 518587–518589, 518592, 518596, and 518598, and unillustrated paratypes, USNM 518599–518621. Illustrated paratypes, not in the measured sample (with collection numbers): USNM 518590 (USGS 4678-SD), 518591 (USGS 11210-SD), 518593 (USGS 11211-SD), 518594 (USGS 11468-SD), 518595 (USGS 5692-SD), and 518597 (11197-SD). Collection localities are described in the Appendix.

Additional studied specimens (unillustrated paratypes) are USNM 519491, 519492 (White Creek, USGS 5692-SD, Stafford Quad.); USNM 519493 (Jaycox Run, USGS 11211-SD, Geneseo Quad.); USNM 519494 (Brown's Creek, USGS 11197-SD, Geneseo Quad.); and USNM 519495 (Schaeffer Creek north of Centerfield, USGS 11468-SD, Canandaigua Quad.). All specimens are from the Centerfield Member (Givetian), Ludlowville Formation, Hamilton Group, in west-central New York. See Appendix for collection locality data.

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## APPENDIX—COLLECTION LOCALITIES

Localities are listed by stratigraphic unit, from oldest to youngest, and from west to east (north to south locally) along the New York outcrop belt shown on the index map (Text-fig. 2). Counties (Co.) are cited for each locality and shown on the figure. Principal map references are to the USGS 7.5 minute quadrangles (Quad.). Numbers ending with -SD are listed in the USGS Silurian-Devonian catalog (copy at U. S. National Museum of Natural History, USNM, Washington, DC). These are collection numbers but also can serve as locality numbers.

The list is a comprehensive catalog of collections and localities for all New York Hamilton specimens on which this study is based (including data for unillustrated specimens of *H. halli halli* in the statistical samples). Specimen numbers (and number of specimens) for *H. halli halli* only, are listed with the appropriate collection; additional unillustrated specimens cited in text are noted. Field data for illustrated specimens are in plate explanations. Comparable data for other taxa are in the *Material* section of the systematic descriptions.

### 1. Halihan Hill Coral Bed

**Westerlo Quad:** USGS 11221-SD, drainage ditch on W side of Cole Hill Rd., 1.5 km S of Bensons Corners (elev. 1282 ft). Albany Co. USNM 518312, 518313 (2 specimens).

**Plattekill (now Woodstock) Quad:** USGS 5305-SD, bed of Plattekill Creek at bridge, 1.2 km W of Mount Marion (or 2.7 km E of High Woods (village) on Glasco Turnpike). Ulster Co. USNM 518314–518322 (9 specimens) plus 3 illustrated and measured.

USGS 11222-SD, same as 5305-SD. USNM 518323 (1 specimen).

**Kingston West Quad:** USGS 11497-SD, cut on S side of US 209 at Sawkill Rd. exit ramp, N of Kingston. Ulster Co. USNM 518324 is "large" specimen mentioned in text.

### 2. Case Hill Coral Bed

**South Onondaga Quad:** USGS 9747-SD, creek on N slope of Case Hill just W of Case Rd.; type locality of Grasso (1986). Onondaga Co. USNM 518329–518341 (13 specimens) plus 4 illustrated and measured.

**Otisco Valley Quad:** USGS 11458-SD, Rattlesnake Gulf on Bare Mountain, just N of Otisco Rd. (on W side of Tully Valley); locality 10 of Grasso (1986). Onondaga Co. USNM 518342–518345 (4 specimens).

### 3. Centerfield Limestone

**Alexander Quad:** USGS 5705-SD, Murder Creek, just W of Harper Rd., 2 km N of Darien. Genesee Co. USNM 518349–518352 (4 specimens).

**Batavia South Quad:** USGS 4678-SD, 3 km E of East Alexander just N of D.L. and W. RR tracks (0.6 km E of Francis Rd.). Genesee Co. USNM 518353–518361 (9 specimens). This exposure is "3 mi W of East Bethany" and is probably the locality of collections USNM 134874 and 134883 (see expl. Pl. 1).

USGS 6061-SD, same as 4678-SD. USNM 518362 (1 specimen).

USGS 11210-SD, RR cuts 5.2 km E of East Alexander, along D. L. and W. RR line, E of Center Rd. Genesee Co. USNM 518363 (1 specimen).

**Stafford Quad:** USGS 5692-SD, 1.6 km E of East Bethany along White Creek; S of D. L. and W. RR and W of Transit Rd. Genesee Co. USNM 518364–518365 (2 specimens).

**Geneseo Quad:** USGS 5324-SD, NW corner of map; Browns Creek, 0.2 km W of Genesee and Wyoming RR bridge over creek. Locality is approximately 1.6 km E of York. Livingston Co. USNM 518366–518372 (7 specimens) plus 2 illustrated (1 of which is not measured).

USGS 5714-SD, same as 5324-SD. USNM 518373–518374 (2 specimens).

USGS 11197-SD, same as 5324-SD. USNM 518375–518378 (4 specimens) plus 1 illustrated.

USGS 11211-SD, Jaycox Creek, 0.15 km NE of Nations Rd. at a point approximately 1.6 km NW of NY 39 and 4+ km N of Geneseo. Livingston Co. USNM 518379 (1 specimen).

**Canandaigua Quad:** USGS 11468-SD, Schaeffer Creek, E of McCann Rd. at a point 1.4 km N of Centerfield (SW corner of map). Ontario Co. USNM 518380–518382 (3 specimens).

**Stanley Quad:** USGS 5683-SD, Wilson Creek under Ross Rd. bridge over creek. (E edge of map, 4.5 km S of Geneva). Ontario Co. USNM 518383 (1 specimen).

**Romulus Quad:** USGS 5375-SD, small quarry, S of road, 0.5 km W of Fayette; Fayette Town quarry. Seneca Co. USNM 518384–518385 (2 specimens).

USGS 11465-SD, same as 5375-SD. USNM 518386–518390 (5 specimens).

### 4. Staghorn Point Coral Bed

**Spafford Quad:** USGS 9093-SD, E shore Skaneateles Lake from Jenny Point to Willow Point. Onondaga Co. USNM 518396–518398 (3 specimens).

USGS 9094-SD, same as 9093-SD. USNM 518399–518400 (2 specimens).

USGS 8763-SD, Staghorn Point, E shore of Skaneateles Lake. USNM 518401–518402 (2 specimens).

USGS 7542-SD, just N of Willow Point, E shore of Skaneateles Lake. USNM 518394–518395 (2 specimens) plus 2 illustrated and measured.

The "Skaneateles Lake" locality of Wells (1937) may have included all of the nearly continuous exposure from north of Jenny Point to Willow Point (2.2 km), but his collecting is thought to have been concentrated near Staghorn Point. PRI 24550 and 24561, "form *praecocius*," are from Wells' collection.

**South Onondaga Quad:** USGS 9102-SD, Ravine on Lords Hill, E of Rt 80, approximately 0.3 km S of US 20. Onondaga Co. 1 specimen, illustrated and measured.

5. Joshua Coral Bed

**Spafford Quad:** The following collection localities are all ravines on the SW side of Otisco Lake. Onondaga Co.

USGS 9122-SD, ravine 2 km NW of old causeway; Joshua 25.7 m thick; collection from lower 5 m. USNM 518407 (1 specimen).

USGS 9123-SD, same ravine as 9122-SD; collection from upper 0.5 m. USNM 518408 (1 specimen).

USGS 9115-SD, ravine 0.2 km NW of old causeway; Joshua 9.6 m thick, collection from lower 5.5 m. USNM 518409 (1 specimen).

USGS 9110-SD, ravine 0.3 km SE of old causeway; Joshua 10 m thick, collection from lower 3.2 m. USNM 518410–518411 (2 specimens).

USGS 5667-SD, same ravine and beds as 9110-SD.

USGS 9114-SD, same ravine as 9110-SD; collection from top 0.6 m. USNM 518412 (1 specimen).

**Otisco Valley Quad:** USGS 9364-SD, ravine on NE side of Otisco Valley near SE end of Otisco Lake, 1.9 km NW of village of Otisco Valley. Onondaga Co. USNM 518413 (1 specimen).

**South Onondaga Quad:** The following collections are from two sections (road cut and ravine) on Lords Hill, S of Lords Corners (on US 20); the road cut thickness is distorted by local faulting (Oliver, 1951); thickness in both sections is probably close to 15 m. The Lords Hill collection(s) of Wells (1937) may be from either of the two sections. Onondaga Co.

USGS 9131-SD, road cuts on NY 80, approximately 0.4 km S of Lords Corners; Joshua 21 m thick (due to faulting). Onondaga Co. 1 specimen, illustrated and measured.

USGS 4669-SD, same as 9131-SD. USNM 518419–518427 (9 specimens) plus 3 illustrated and measured.

USGS 8783-SD, cornfield (currently apple orchard), estimated 0.3 km E of NY 80, just W of upper end of ravine; repeated ploughing of field over a period of several years produced our largest collection of Joshua *Heliophyllum*, presumably from the uppermost part of the coral bed as the ravine exposure is 14 m thick and only slightly lower. Onondaga Co.

USGS 8762-SD, same as 8783-SD. USNM 518414–518418 (5 specimens).

6. Darien Coral Bed

**Alexander Quad:** USGS 5706-SD, Murder Creek, 1 km NNW of US 20 in Darien, and 0.1 km S of Sharrack Rd. Genesee Co. USNM 518432–518439 (8 specimens) plus 1 illustrated and measured.

USGS 11208-SD, same as 5706-SD. USNM 518440 (1 specimen) plus 3 illustrated and measured.

The specimens illustrated on Plate 1, figures 1–10 (exterior views) are probably from this coral bed and locality.

7. Jaycox Member, Greens Landing Coral Bed

**Buffalo SE Quad:** Erie Co. See Tichenor Member.

**East Aurora Quad:** USGS 5708-SD, Buffalo Creek, just N of Bullis Rd. bridge, 3.6 km W of Marilla (loc. 4 of Baird, 1979). Erie Co. USNM 518445–518449 (5 specimens) plus 1 illustrated and measured. PRI 40200, illustrated on Plates 12 and 13, is from this locality.

**Corfu Quad:** USGS 5703-SD, Peck Creek S of US 20 and just N of Erie or D, L & W RR tracks, 3.4 km E of Alden (1.1 km E of County Line Road). Genesee Co.

USGS 5704-SD, Elevenmile Creek on S side of US 20 (loc. 5 of Baird, 1979). Genesee Co. USNM 518450–518451 (2 specimens).

**Stafford Quad:** the USNM locality "Tichenor; 1.5 mi SE of East Bethany" (see Pl. 7 explanation) is from the west branch of White Creek between US 20 and NY 63 (loc. 9 of Baird, 1979); the specimen (illustrated but not measured) is probably from the Jaycox Member. Genesee Co.

USGS 5693-SD, small cut on Transit Road, discussed more fully as a Deep Run locality (*q.v.*). A loose specimen of *H. halli confluens* was thought to be from deeply weathered Tichenor when collected (July 1960) but might have come from Jaycox beds disturbed during road building. Genesee Co.

**Leroy Quad:** Hill's Gulch, or Hill Farm, waterfall 0.3 km W of Asbury Rd. and 0.4 km S of US 20 (loc. 10 of Baird, 1979); see also lower Deep Run collection list. Tichenor Limestone forms waterfall with lower Deep Run well exposed above and Jaycox below; the old USNM locality 134884 specimens on Plate 1 may be from either or both units. None of our illustrated

or measured specimens is from the Jaycox at this locality. Genesee Co.

USGS 5323-SD, at S edge of map; Browns Creek, 1.9 km W of York (NY 36, at edge of map). This is the "west of York" locality, source of many collections over many years. Livingston Co. USNM 518452 (1 specimen) plus 1 illustrated and measured.

USGS 5715-SD, same as 5323-SD. USNM 518453 (1 specimen).

USGS 11196-SD, same as 5323-SD. USNM 518454–518459 (6 specimens).

Specimen USNM 519490, cited in discussion of *External features* of *H. halli confluens,* is from this locality.

**Geneseo Quad:** Jaycox Run, approximately 0.5 km W of NY 39 at a point 4.7 km NNE of US 20A in Geneseo. USNM 487251, "form *praecoquus,*" collected by G. Kloc (Pl. 12, figs. 9–10) is from this locality. Livingston Co.

**Canandaigua Lake Quad:** USGS 5687-SD, Tichenor Gully on W side of Canandaigua Lake. Ontario Co. USNM 518460 (1 specimen).

USGS 11470-SD, Greens Landing ravine on E side of Canandaigua Lake, near E edge of map. Ontario Co. USNM 518461–518466 (6 specimens) plus 2 illustrated and measured. One "form *praecoquus*" from this collection is illustrated on Plate 12, figs. 2–4 (USNM 518541).

Tichenor Limestone Member

**Buffalo SE Quad:** USNM loc. 1014, "N. branch of Smoke Creek, just E of Berg Road Bridge, SE of Buffalo," Erie Co. USNM 133683 is specimen cited in discussion of *H. halli confluens* as representing an occurrence in the Tichenor, west of the known limit of the Jaycox Member.

8. Lower Deep Run Member

Localities for the colonial *Heliophyllum delicatum* were described by Oliver and Sorauf (1994); these are repeated here only for the three specimens illustrated on Plate 29 and for the *H. halli halli* that are illustrated and/or part of the statistical sample.

**Corfu Quad:** USGS 5703-SD, Peck Creek, 3.4 km E of Alden, 0.5 km S of US 20, near Erie RR bridge over creek. (Loc. 2 of Oliver and Sorauf). Genesee Co.

**Stafford Quad:** USGS 5693-SD, Transit Road, 1.1 km N of NY 63 intersection. (Same as 11481-SD, loc. 4 of Oliver and Sorauf). Genesee Co. A small roadcut exposes a complete Deep Run section (measured in July 1990) as follows (compare with Text-fig. 1):

Menteth Limestone 17 cm.

Deep Run Shale 46 cm (corals common including *H. delicatum,* characteristic of member and *H. halli halli*) Tichenor Limestone 29 cm (poorly exposed). A loose specimen of *H. halli confluens* is thought to have come from the Tichenor or Jaycox although the latter was not exposed. The following are almost certainly from the Deep Run: USNM 518475–518479 (5 specimens) plus 1 illustrated and measured. USNM 518480–518482 (3 specimens) are examples of "*praecoquus*" cited in discussion (not illustrated or in measured sample). See discussion of this locality in Jaycox collections section.

USGS 4676-SD, creek bed (tributary of Oatka Creek) 1 km SSE of Pavilion Center, and approximately 0.3 km SW of Rogers Rd. (Loc. 5 of Oliver and Sorauf). Genesee Co. USNM 518483–518484 (2 specimens).

**Leroy Quad:** USGS 5698-SD, Hill's Gulch, or Hill Farm, waterfall 0.3 km W of Asbury Rd. and 0.4 km S of US 20; see also notes in the Jaycox Member collection list. Collection is from lower Deep Run above the Tichenor Ls. (Loc. 6 of Oliver and Sorauf). Genesee Co. USNM 518485 (1 specimen) plus 2 illustrated and measured.

**Honeoye Quad:** USGS 11491-SD, West Bloomfield Twp. in branch of Beebe Creek that passes Taft Rd. just S of elevation 870 ft; 0.5 km W of Taft Rd. (Loc. 8 of Oliver and Sorauf). Collected by D. Griffing. Livingston Co.

**Canandaigua Lake Quad:** USGS 5691-SD, unnamed gully, 1.2 km N of Tichenor Point on W side of Canandaigua Lake; approximately 0.2 km W of West Lake Rd. (Loc. 9 of Oliver and Sorauf). Ontario Co.

USGS 11473-SD, Tichenor Gully on W side of Canandaigua Lake, approximately 0.25 km W of West Lake Rd. (Loc. 10 of Oliver and Sorauf). Ontario Co. 1 specimen, illustrated and measured.

USGS 11475-SD, lake shore, 0.9 km S of creek at Tichenor Point, W side of Canandaigua Lake. Ontario Co. USNM 518486 (1 specimen) plus 2 illustrated (1 not in measured sample).

**Rushville Quad:** USGS 5684-SD, W edge of map; Greens Landing Ravine on E side of Canandaigua Lake (enter from E side of Canandaigua Lake Quad.); Tichenor Ls. exposed near boundary of quads., Deep Run is approximately 0.1 km east of boundary. (Loc. 13 of Oliver and Sorauf). Ontario Co. 1 illustrated and measured specimen.

**Geneva South Quad:** USGS 11490-SD, Kashong Glen, W side of Seneca Lake, approximately 1.5 km W of NY 14. (Loc. 17 of Baird, 1979). Ontario Co. USNM 518487 (1 specimen) plus 1 illustrated but not measured.

**Dresden Quad:** USGS 11489-SD, E shore of Seneca Lake 1 km NNW of Indian Creek (N boundary of

cemetery on N side of Willard). (Loc. 15 of Oliver and Sorauf). Seneca Co. USNM 518488 (1 specimen) plus 1 illustrated and measured.

Bay View Coral Bed

**Buffalo SE Quad:** USGS 9140-SD, large, low abandoned quarry N of Big Tree Rd. and W of old Erie RR position; 1.5 km S of Blasdell. See discussion in section on the Fall Brook population. Erie Co.

9. Fall Brook Coral Bed

**Leicester Quad:** All of our collections are from one locality north of Leicester (formerly Moscow); Livingston Co. The different collections were made at different times. The neotype was stated to be from Moscow, Livingston County. This is probably the Fall Brook coral bed and possibly the Little Beards Creek locality.

USGS 5700-SD, east side of Little Beards Creek in farmyard 0.7 km E of NY 36 and 1.3 km N of Leicester (US 20A). Livingston Co. USNM 518492–518505 (14 specimens) plus 2 illustrated and measured.

USGS 8770-SD, same as 5700-SD. USNM 518506 (1 specimen) plus 1 illustrated and measured.

USGS 11476-SD, same as 5700-SD. Collected by P. E. Cloud. USNM 518507–518508 (2 specimens).

Lansing Coral Bed

**Ludlowville Quad:** USGS 5678-SD, large abandoned quarry above Portland Point, N of Gulf Creek. Tompkins Co. USNM 518509–518514 (6 specimens) make up the sample compared to the Fall Brook sample in discussion of the latter.

10. Bellona Coral Bed, Tully Limestone

**Stanley Quad:** USGS 5341-SD, Kashong Creek in Bellona, upstream from falls, SW of Pre-emption Road bridge. (Loc. 9c of Heckel, 1973). Yates Co. (NE corner). USNM 518520–518528 (9 specimens) plus 1 illustrated and measured.

USGS 8766-SD, same as 5341-SD. 1 illustrated specimen, not in measured sample.

USNM 113668, illustrated by Ehlers and Stumm (1953), is "Kashong Creek, Bellona, N.Y., collected by G.A. Cooper."

Locality USNM 11671, "Yates County, N.Y." is most likely Kashong Creek in Bellona. USNM 518529–518531 (3 specimens) plus 1 illustrated and measured.

USGS 11204-SD, old quarry, 2.1 km N of Bellona. Probably loc. 9n of Heckel, 1973. Ontario Co. USNM 518532 (1 specimen) plus 1 illustrated and measured.

**Ovid Quad:** USGS 5344-SD, Old Chamberlain Quarry, 2.7 km NNE of Ovid. (Loc. 8ab of Heckel, 1973). Seneca Co. USNM 518533–518534 (2 specimens).

USGS 5718-SD, same as 5344-SD. USNM 518535 (1 specimen).

**Scipio Center Quad:** J.W. Wells colln., Scipio Town Quarry, 1.35 km N of Scipio Center. (Loc. 5c of Heckel, 1973). Cayuga Co. USNM 518536 (1 specimen).

**Owasco Quad:** Loc. 5t of Heckel (1973); glen, 1.1 mi (2 km) northwest of Twelve Corners (upstream from bridge). Collected by P. H. Heckel. Cayuga Co.

**Spafford Quad:** USGS 6094-SD, Carpenter Falls on Bear Swamp Creek, 1.7 km SW of mouth of creek (at Carpenter Point, SW side of Skaneateles Lake). (Loc. 5p of Heckel, 1973). Cayuga Co. USNM 518537–518540 (4 specimens) plus 1 illustrated and measured.

## EXPLANATION OF PLATES

Transverse sections of solitary forms are oriented with cardinal septum (if known) toward the top of the page; where not known, an interpretation, based on examination of section and specimen is used. All "sections" are thin sections. Most are photographed as though looking down from the calice; those photographed as though from below are marked UD (upside down). Collection localities (USGS 0000-SD) are in New York State unless otherwise indicated.

## EXPLANATION OF PLATE 1

Figure — Page

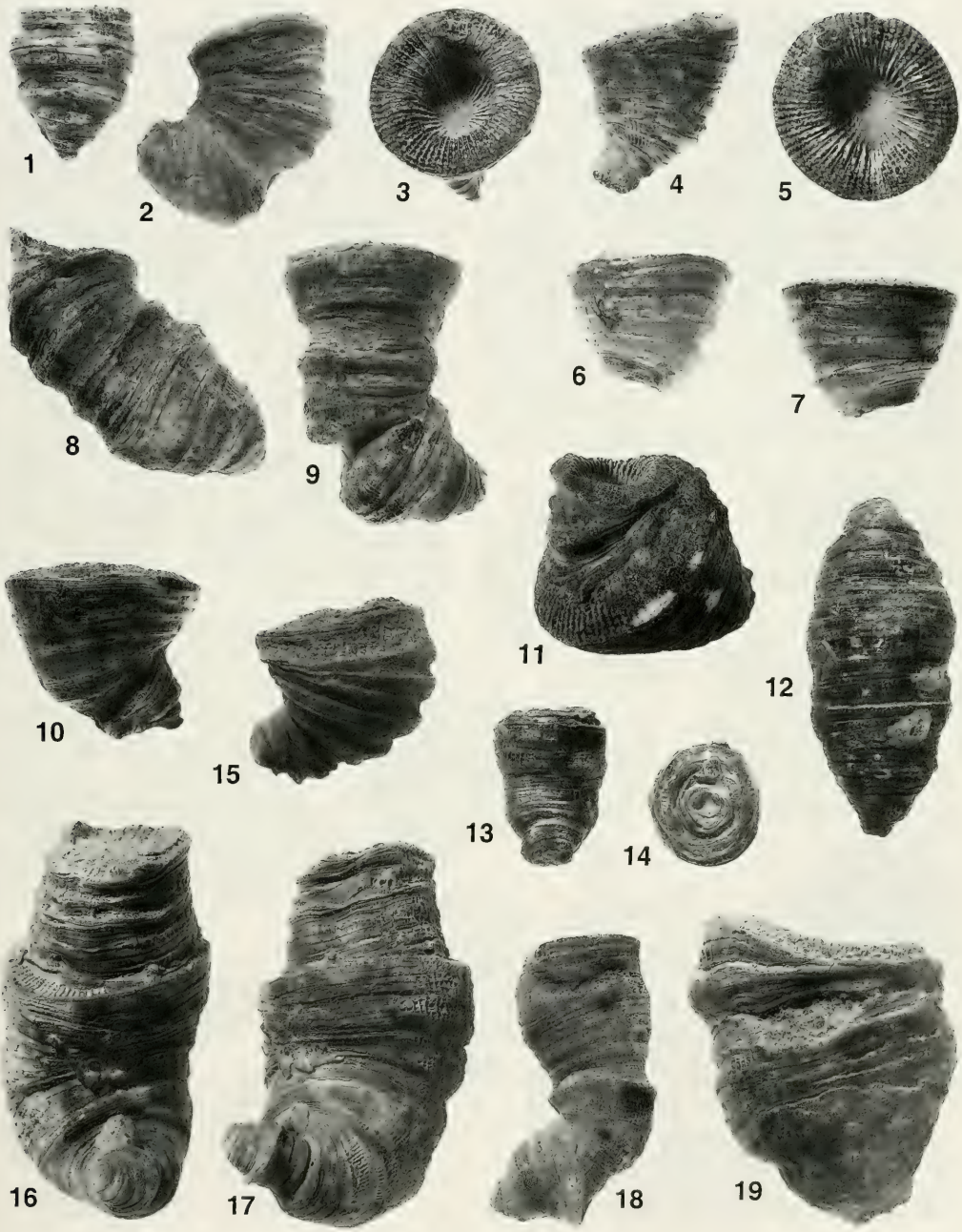
1–19. ***Heliophyllum halli halli*** Milne-Edwards and Haime; exterior views (×1); specimens are from old USNM collections (USNM collection numbers in parentheses) and were selected to illustrate form variation. . . . . 18

1–10. "Wanakah Shale, *Pleurodictyum* bed, Murder Creek, Darien." Almost certainly our Darien coral bed (population 6; see USGS 5706-SD). 1. USNM 518302 (113933); 2. USNM 518303 (72718); 3, 4. USNM 518304 (113933); 5–7. USNM 918305 (133936); 8. USNM 518306 113934); 9. USNM 509792 (72718); 10. USNM 518307 (113936).

11–14. "Hill Farm near Pavilion." (134884). This is our Hill's Gulch locality in the town of Pavilion, but both Jaycox Shale and lower Deep Run crop out there (populations 7 and 8) and the specimens may be from either or both units; see discussion in Appendix—Jaycox, Leroy Quad. 11. USNM 509791; 12. USNM 509793; 13, 14. USNM 518308.

15–19. "Centerfield Member, 3 mi west of East Bethany." This is our population 3 and probably our Francis Road locality (see USGS 4678-SD). 15. USNM 518299 (134874); 16, 17. USNM 509789 (134883); 18. USNM 518300 (134874); 19. USNM 518301 (134874).

Figures 9, 11, 12, and 16–17 are from Sorauf (2001).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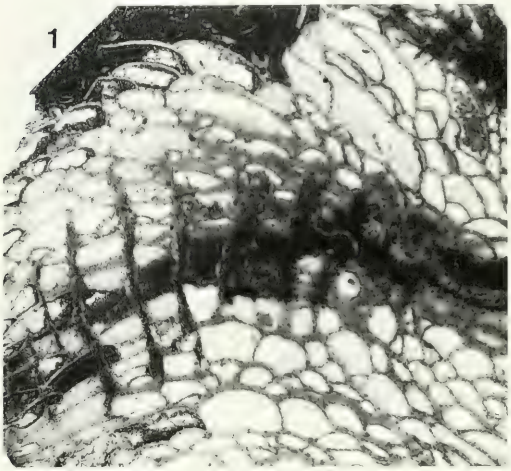
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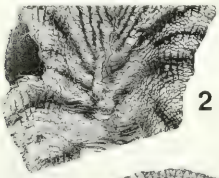
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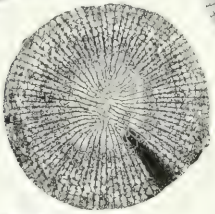
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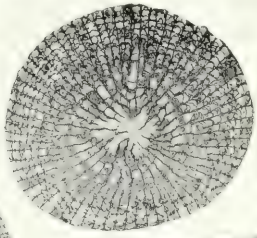
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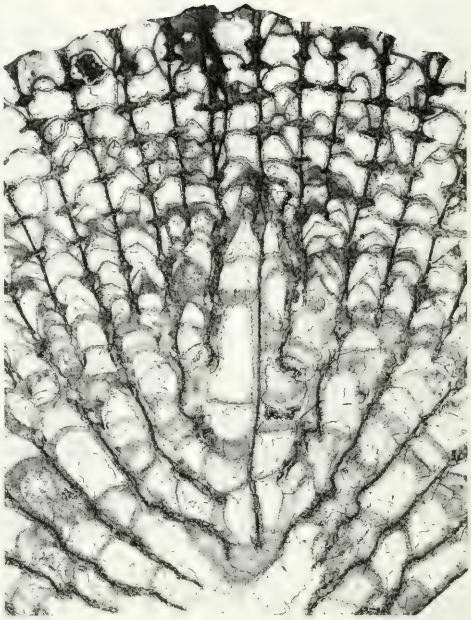
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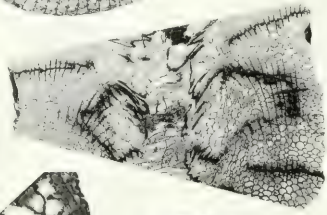
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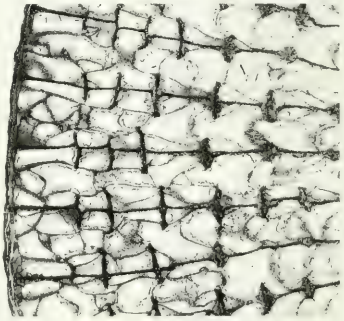
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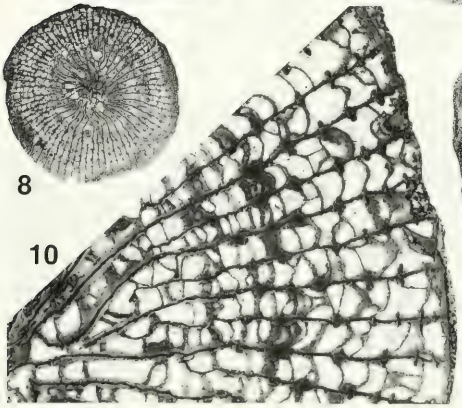
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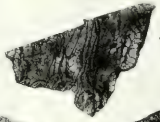
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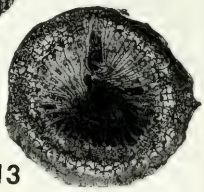
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## EXPLANATION OF PLATE 2

Figure — Page

1–7. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Case Hill coral bed (population 2), USGS 9747-SD, Case Hill. . . . . 18

1–3. USNM 518325; 1, 2. longitudinal (×10, ×1.5) and 3. transverse (×1.5) sections.

4, 5. USNM 518326; transverse (UD) sections (×1.5, ×7.5).

6. USNM 518327; longitudinal section (×1.5).

7. USNM 518328; transverse section (×7.5).

8–13. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Halihan Hill coral bed (population 1), USGS 5305-SD, Mount Marion. . . . 18

8. USNM 518309, transverse (UD) section (×1.5).

9, 10. USNM 518310, longitudinal (×1.5) and partial transverse (UD; ×7.5) sections.

11–13. USNM 518311, longitudinal and lower (UD) and upper transverse sections (approximately 3 mm apart) (all ×1.5).

## EXPLANATION OF PLATE 3

Figure — Page

1–7. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Staghorn Point coral bed (population 4). . . . . 18

1–6. USGS 7542-SD, Skaneateles Lake. 1–3. USNM 518391; transverse (×1.5, ×10) showing short and discontinuous minor septa, and longitudinal (×1.5) sections. 4–6. USNM 518392; upper transverse, intermediate longitudinal, and lower transverse (UD) sections (all ×1.5).

7. USNM 518393, USGS 9102-SD, Lords Hill; longitudinal section through calice of specimen with reflexed margin (×1.5).

8–11. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Centerfield Member (population 3), east of York. . . . . 18

8. USNM 518346, USGS 5324-SD; longitudinal section (×1.5) of unusually large specimen.

9, 10. USNM 518347, USGS 11197-SD; transverse sections (UD; ×1.5, ×7.5).

11. USNM 518348, USGS 5324-SD; transverse section (×1.5).

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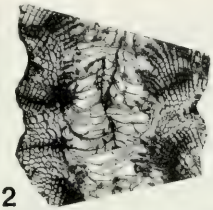
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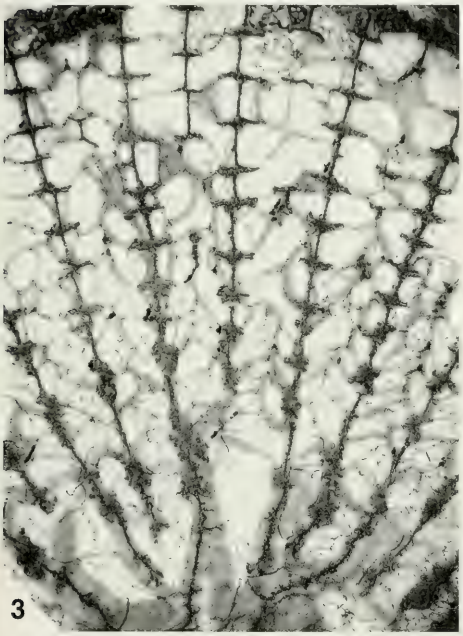
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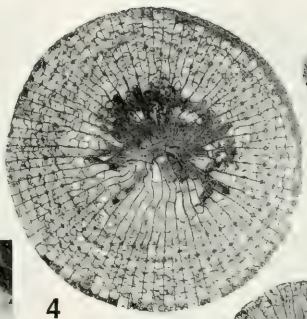
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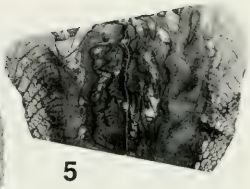
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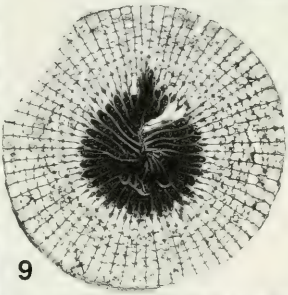
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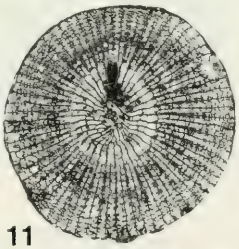
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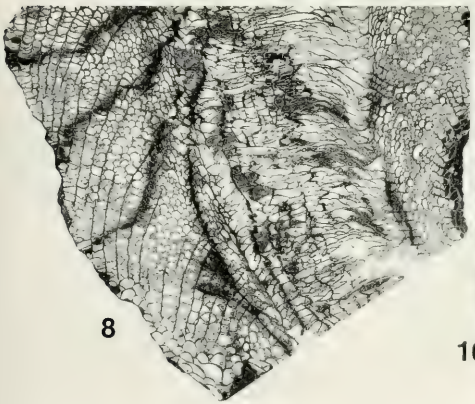
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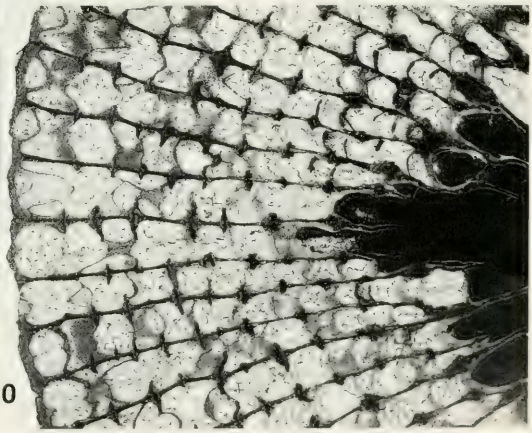
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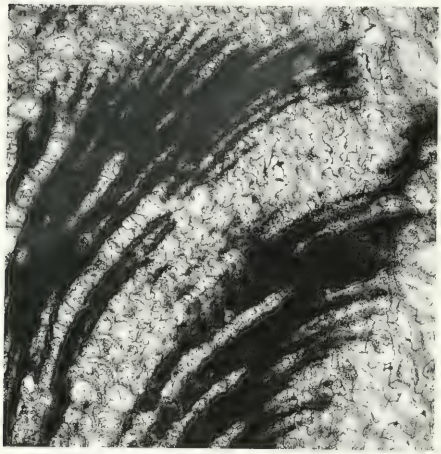
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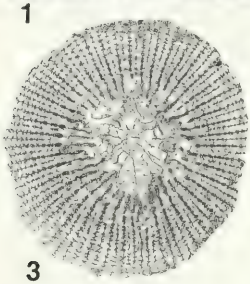
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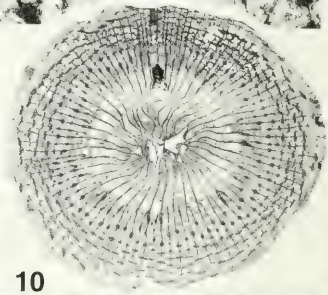
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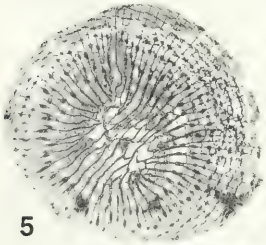
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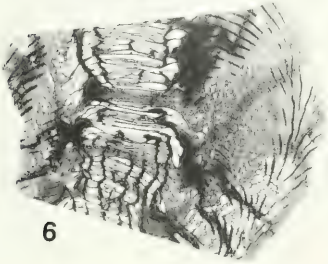
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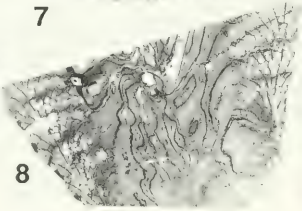
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## EXPLANATION OF PLATE 4

Figure — Page

1–10. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Joshua coral bed (population 5); Lords Hill. . . . . 18

1, 2. USNM 219922, USGS 4286-SD; longitudinal and transverse sections (×10), illustrating Type III carinae (fig. 2 is after Sorauf and Oliver, 1976).

3, 4. USNM 518403, USGS 4669-SD; transverse (UD) and longitudinal sections (×1.5).

5, 6. USNM 518404, USGS 4669-SD; transverse (UD) and longitudinal sections (×1.5).

7, 8. USNM 518405, USGS 9131-SD; transverse (UD) and longitudinal sections (×1.5).

9, 10. USNM 518406, USGS 4669-SD; transverse sections (×1.5, ×5).

## EXPLANATION OF PLATE 5

Figure Page

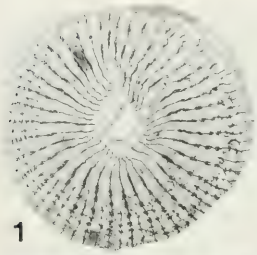
1–9. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Darien coral bed, Murder Creek, Darien (population 6). . . . . 18

1–3. USNM 518428, USGS 5706-SD; transverse (UD; ×1.5, ×7.5) and longitudinal (×7.5) sections illustrating short and discontinuous minor septa and Type IIb carinae.

4, 5. USNM 518429, USGS 11208-SD; longitudinal and transverse sections (×1.5), the latter with short and discontinuous minor septa.

6, 7. USNM 518430, USGS 11208-SD; transverse (UD) and longitudinal sections (×1.5); note long, peripherally discontinuous minor septa and Type IIb carinae.

8, 9. USNM 518431, USGS 11208-SD; transverse sections (UD; ×1.5, ×7.5); minor septa relatively long; figure 9 illustrates "network" dissepimentarium discussed in text.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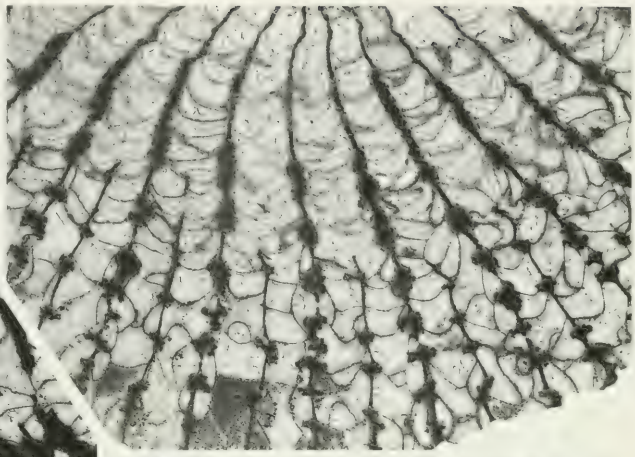
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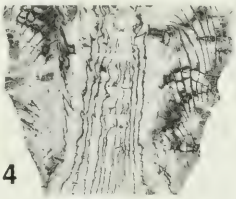
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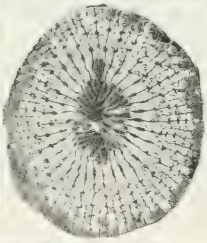
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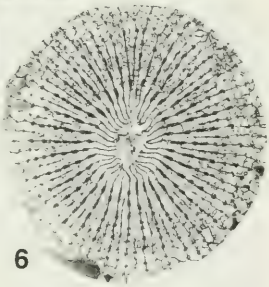
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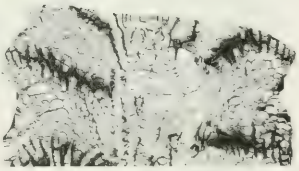
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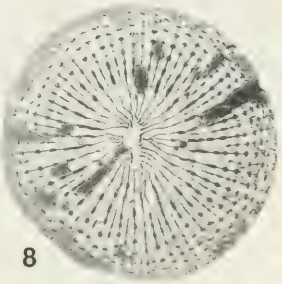
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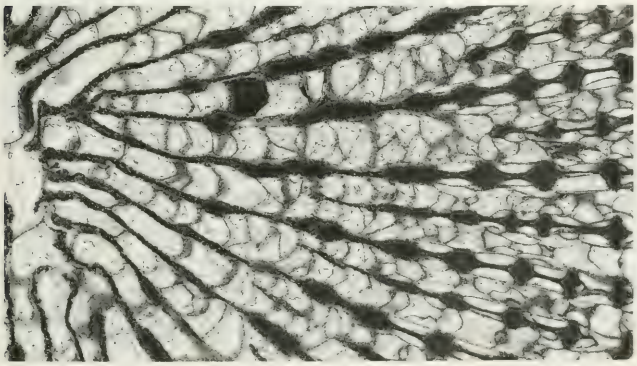
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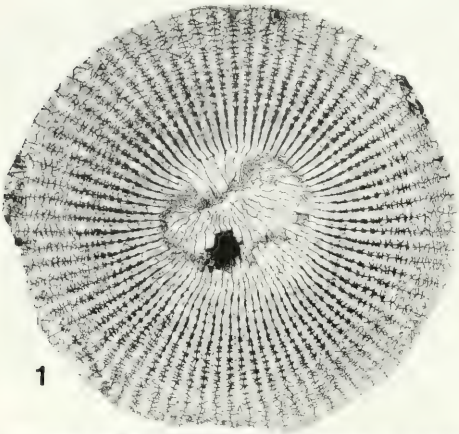
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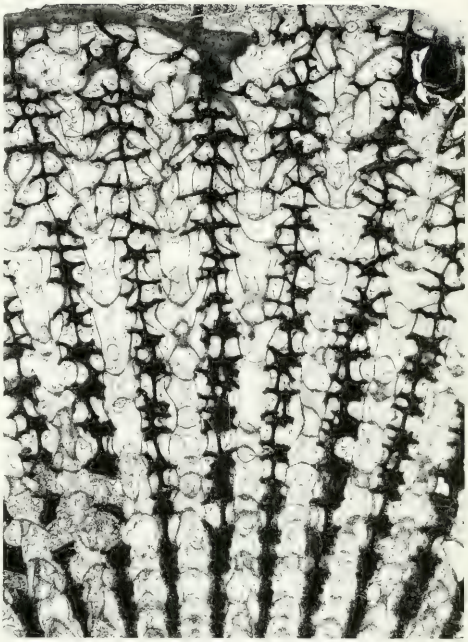
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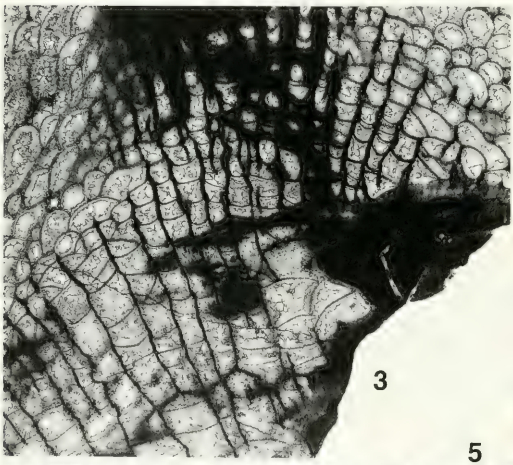
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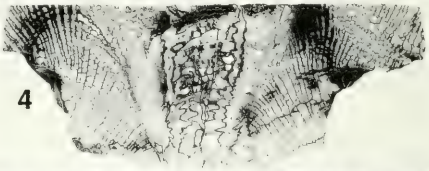
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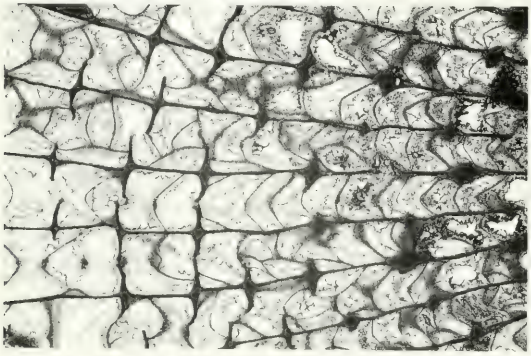
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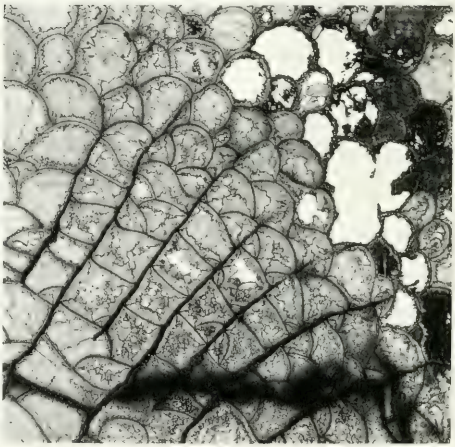
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## EXPLANATION OF PLATE 6

Figure Page

1–6. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Greens Landing coral bed, Jaycox Member (population 7); USGS 11470-SD, Greens Landing ravine on Canandaigua Lake, N.Y.; two specimens with contrasting carinae. . . . . 18

1–4. USNM 518441; transverse and longitudinal sections (×1.5) and details of each (×7.5); Type I→III carinae.

5, 6. USNM 518442; parts of transverse (UD) and longitudinal sections (×7.5); simple, Type I carinae.

## EXPLANATION OF PLATE 7

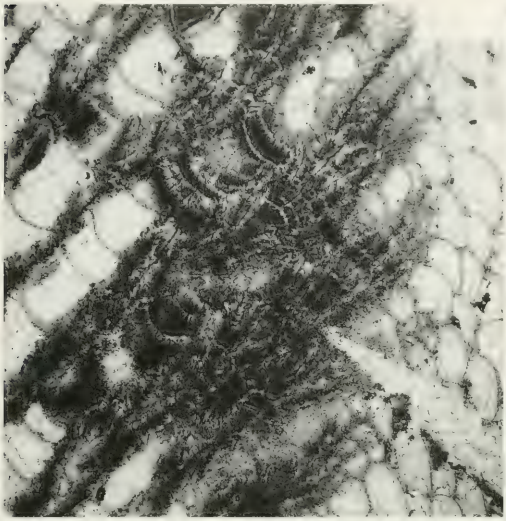
Figure — Page

1, 2. ***Heliophyllum halli halli*** Milne-Edwards and Haime. USNM 219925; specimen is from an old USNM collection "Hamilton, Ludlowville, Tichenor; 1.5 miles SE of E. Bethany." The locality is the west branch of White Creek and the specimen is probably from the Greens Landing coral bed, Jaycox Member (population 7), because the richly fossiliferous beds beneath the Tichenor Limestone were long included in the Tichenor. However, the Deep Run Shale (with population 8) overlies the Tichenor at this locality and this is a possible source. Two details of longitudinal section (×10) to illustrate Type IIa carinae (compare these with Type IIb on Plate 8); for additional illustrations of same specimen, see Sorauf and Oliver (1976, pl. 3, figs. 2–4). . . . . 18

3–5. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Greens Landing coral bed, Jaycox Member (population 7). . . . . 18

3. USNM 518443, USGS 5708-SD, Bullis Bridge; detail of longitudinal section (×10) with Type IIb carinae.

4, 5. USNM 518444, USGS 6108-SD, west of York; transverse and longitudinal sections (×1.5) showing Type I and I→III carinae.



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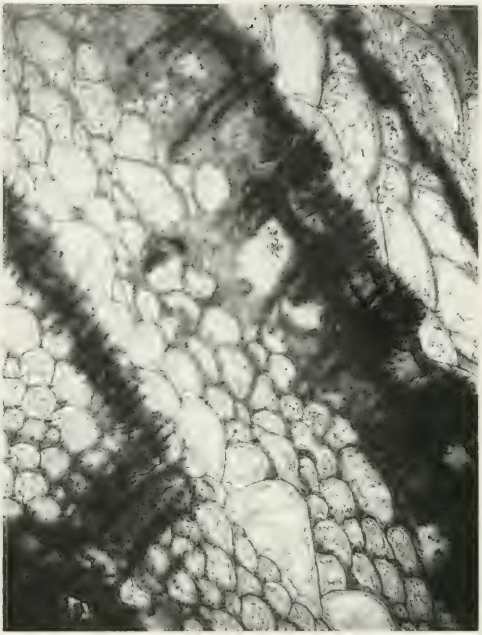

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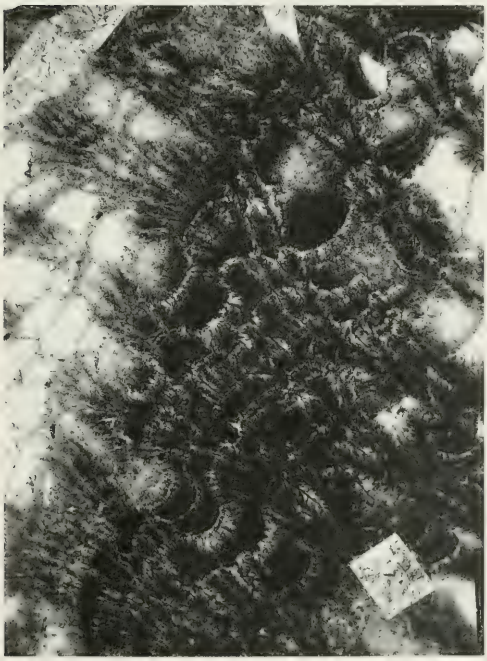

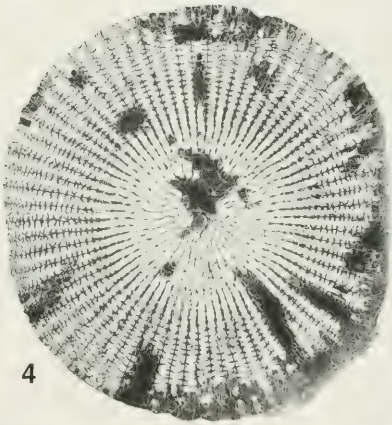

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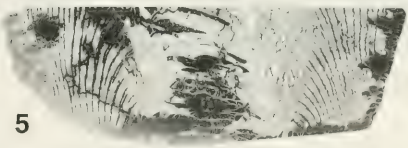

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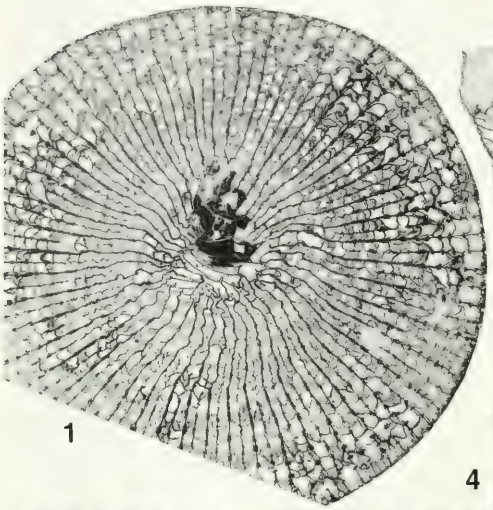

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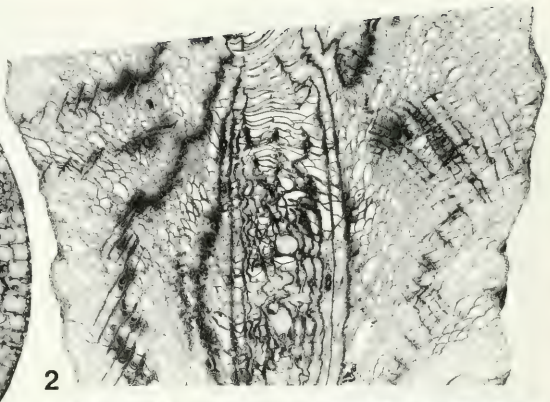

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## EXPLANATION OF PLATE 8

Figure — Page

1–5. ***Heliophyllum halli halli*** Milne-Edwards and Haime; lower Deep Run Shale (population 8). USNM 498542, USGS 5684-SD, Deep Run ravine on Canandaigua Lake.

1–2. transverse and longitudinal sections (×2); photographs of these two sections were published by Sorauf and Oliver (1976, text-fig. 2) with erroneous stratigraphic and locality data, here corrected.

3. detail of another transverse section with peripheral discontinuities in minor and some major septa (×7.5).

4. detail of Type IIb carinae in upper right of figure 2; vepreculae (arrows) are the outer ends of secondary trabeculae approximately perpendicular to section (×10).

5. detail of another longitudinal section with Type IIb carinae (×15). Compare Type IIb carinae illustrated here to Type IIa on Plate 7. . . . . 18

## EXPLANATION OF PLATE 9

Figure — Page

1–14. ***Heliophyllum halli halli*** Milne-Edwards and Haime; lower Deep Run Shale (population 8); from various localities in western and west-central N.Y.; all · 1.5. . . . . 18

1–3. USNM 518467, USGS 11475-SD, Canandaigua Lake; upper and lower (UD) transverse and intermediate longitudinal sections.

4, 5. USNM 518468; USGS 11473-SD, Canandaigua Lake; upper and lower transverse sections.

6, 7. USNM 518469, USGS 5693-SD, Transit Road; transverse and longitudinal sections.

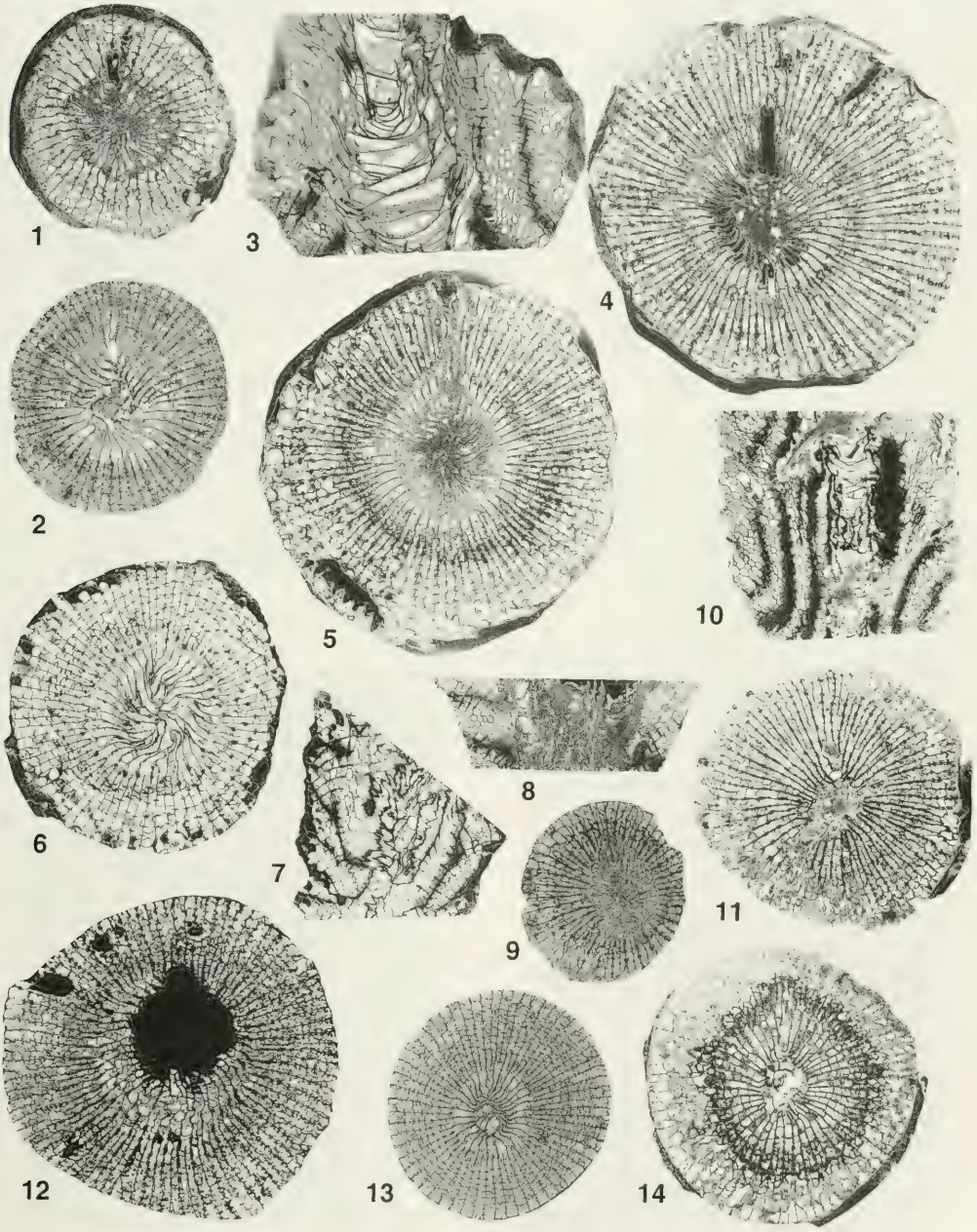
8, 9. USNM 518470, USGS 11475-SD, Canandaigua Lake; longitudinal and lower transverse sections of immature individual.

10, 11. USNM 518471, USGS 5698-SD, Hill's Gulch; longitudinal and transverse sections with Type IIb carinae producing vepreculae.

12. USNM 518472, USGS 11490-SD, Kashong Glen; transverse section through calice showing cardinal fossula.

13. USNM 518473, USGS 11489-SD, Seneca Lake; transverse section with long, complete minor septa.

14. USNM 518474, USGS 5698-SD, Hill's Gulch; transverse section (UD).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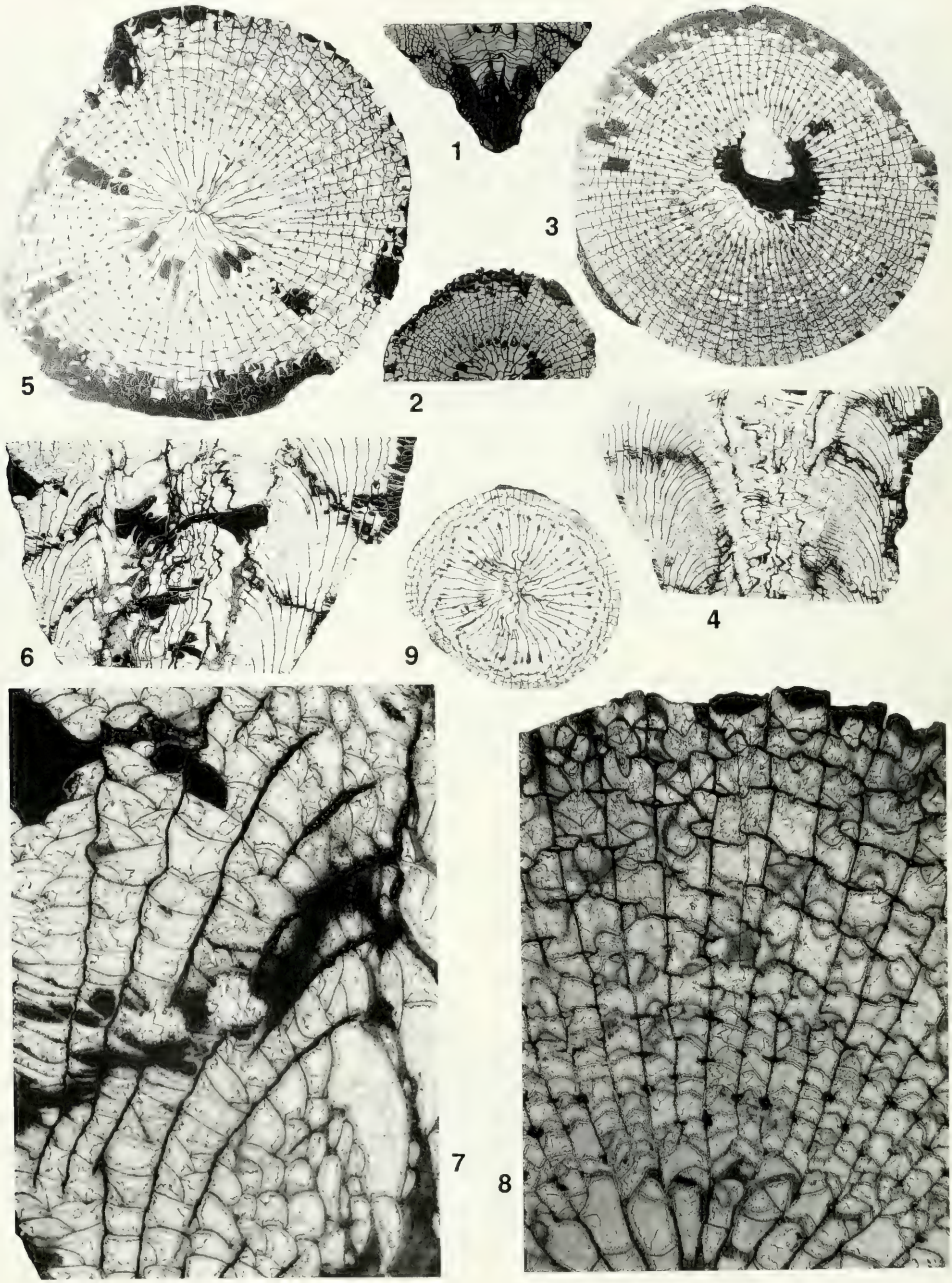
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## EXPLANATION OF PLATE 10

Figure — Page

1, 2. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Neotype, MNHN IP S.11661 (Paris); longitudinal and transverse sections (×1.5); specimen illustrated by Milne-Edwards and Haime (1851, pl. 7, figs.6, 6a, 6b) and Coen-Aubert (1987, pl. 1, figs. 1, 2). Locality given as Hamilton Group, Moscow (now Leicester), Livingston County, New York; this is probably the Fall Brook coral bed (our population 9), and may be our Little Beards Creek locality. . . . . 18

3–9. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Fall Brook coral bed (population 9); Little Beards Creek, north of Leicester. . . . 18

3, 4. USNM 518489, USGS 5700-SD; transverse and longitudinal sections (×1.5).

5–8. USNM 518490, USGS 8770-SD; transverse (UD) and longitudinal sections (×1.5), and parts of same (×7.5, ×5).

9. USNM 518491, USGS 5700-SD; transverse section (UD).

Note that virtually all carinae are simple Type I.

## EXPLANATION OF PLATE 11

Figure — Page

1–8. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Bellona coral bed, Tully Limestone (population 10); Bellona and other localities in central N.Y. . . . . 18

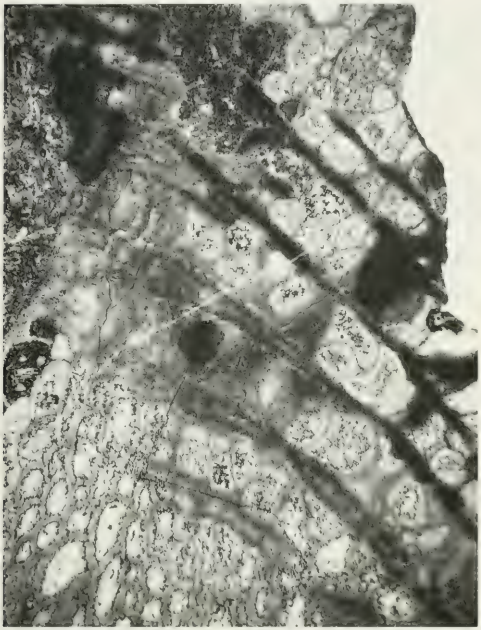
1, 2. USNM 518515, USGS 5341-SD, Bellona; longitudinal section (×1.5) and part of same (×10) with Type I→III carinae.

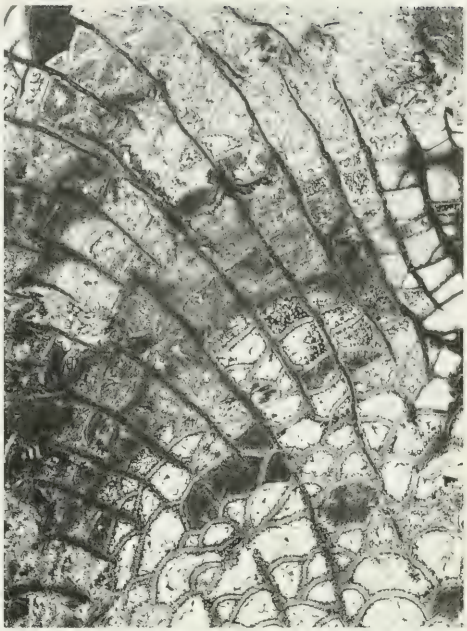
3, 4. USNM 518516, USGS 11204-SD, Bellona; part of longitudinal (×7.5) and transverse (UD; ×1.5) sections, with Type I carinae.

5. USNM 518517; Yates County, probably Bellona; transverse section (UD; ×1.5).

6. USNM 518518; USGS 8766-SD, Bellona; transverse section through immature growth stage with partial dilation (×1.5).

7, 8. USNM 518519; USGS 6094-SD, Carpenters Falls; longitudinal section (×1.5, and detail ×10) showing Type IIb carinae.





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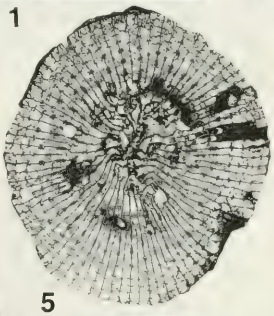

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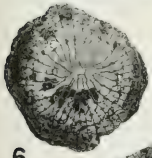

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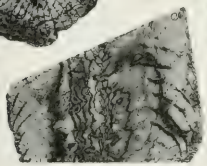

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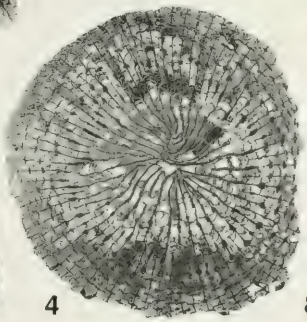

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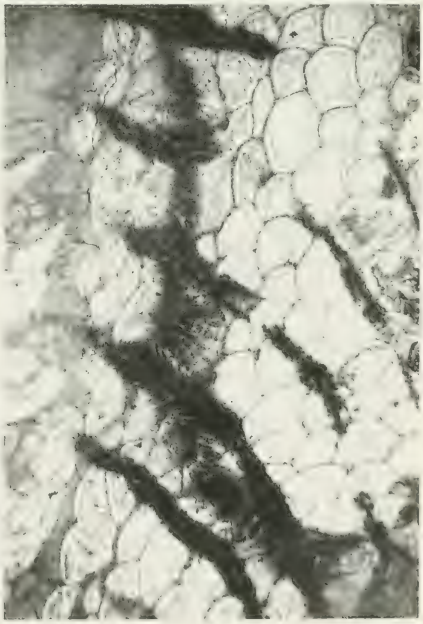

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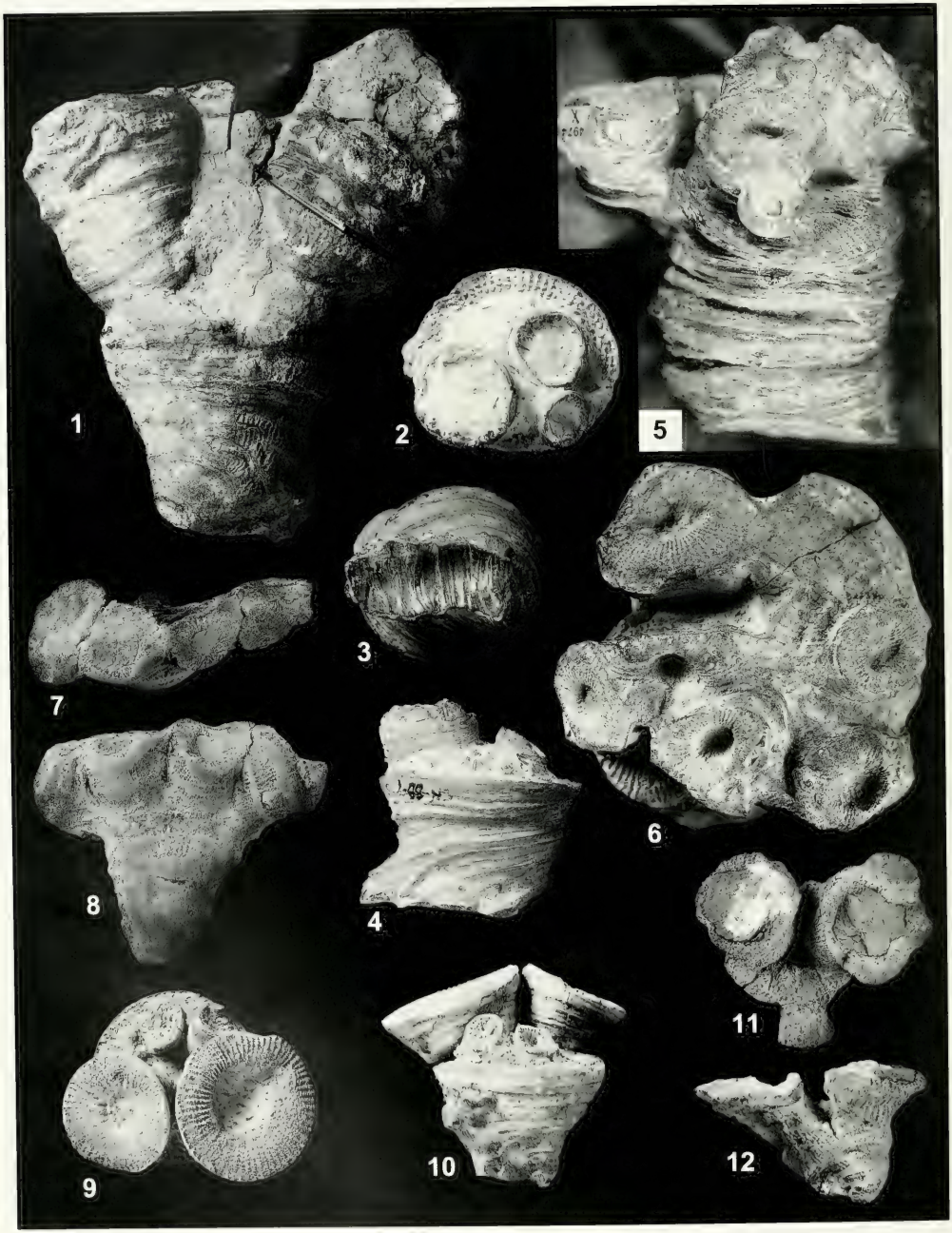
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## EXPLANATION OF PLATE 12

Figure — Page

1–12. ***Heliophyllum halli halli*** Milne-Edwards and Haime; Exterior views of specimens with offsets, including "forma *praecoquus*" of Wells (1937). (×1, except fig. 1). . . . . 18

1. PRI 40200 (coll. E.J. Buehler); Jaycox Shale, Bullis Bridge, Green's Landing coral bed (our population 7); (×0.9); protocorallite is nearly complete with apex to lower left, photograph shows large apical angle of protocorallite and offsets (see also Pl. 13).

2–4. USNM 518541, USGS 11470-SD, Greens Landing ravine, Jaycox Member, Greens Landing coral bed (population 7); 2. top view of calice and three offsets; 3. basal view showing scar of attachment to another coral; 4. side view.

5, 6. AMNH 517220; Hamilton Group, Livingston County (probably Jaycox or younger); side and top views of *Heliophyllum proliferum* of Hall (1877, pl. 26, fig. 5) (see also Pl. 13).

7, 8. PRI 24550; Staghorn Point coral bed (our population 4), Skaneateles Lake; top and side views of *H. halli* "forma *praecoquus*" ("holotype" of Wells, 1937, pl. 1, fig. 12, and text-fig. 10).

9, 10. USNM 487251; Jaycox Member, Green's Landing coral bed, Jaycox Run (collected, prepared, and given to USNM by G. Kloc); top and side views of near-perfect specimen of "*forma praecoquus*".

11, 12. PRI 24561; Staghorn Point coral bed (our population 4), Skaneateles Lake; top and side views of "forma *praecoquus*" of Wells (1937, text-fig. 11).

In addition to cited illustrations, specimens in figures 1 and 7–10 were illustrated by Oliver (1997a, pl. 1).

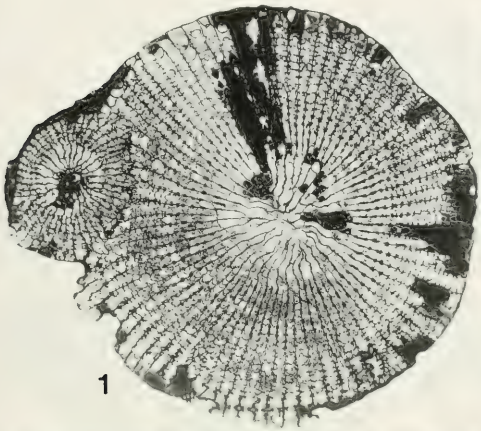
## EXPLANATION OF PLATE 13

Figure — Page

1–7. ***Heliophyllum halli halli*** Milne-Edwards and Haime; thin sections of two specimens with offsets illustrated on Plate 12. . . . . 18

1–4. AMNH 517220 (see explanation of Pl. 12, figs. 5, 6); 1. transverse section (×1.5) just below the crowd of offsets in Plate 12, figures 5, 6; 4. longitudinal section (1.5) from lower end of specimen as shown in Plate 12, figure 5; 2, 3 (×10); 2. detail of figure 1; 3. detail of figure 4 showing Type III carinae.

5–7. PRI 40200 (see explanation of Pl. 12, fig. 1); 5. transverse section (×2.5) through calice of protocorallite and lower ends of offsets; 7. transverse section (×1.5) approximately 1 cm lower than the one in figure 5; 6. longitudinal section (×1.5) from below transverse sections.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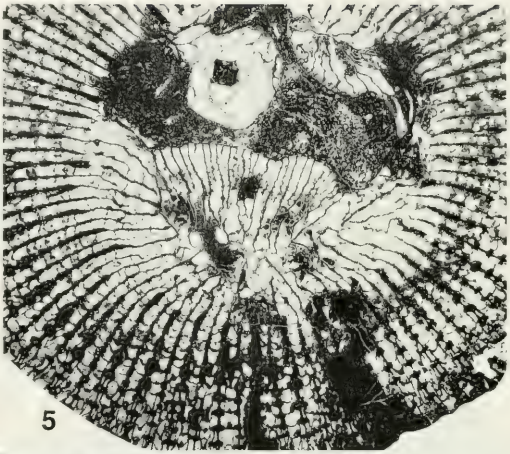
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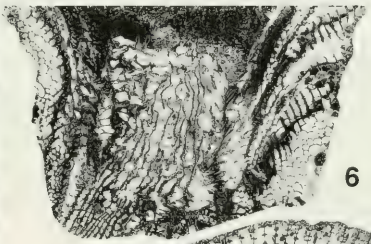
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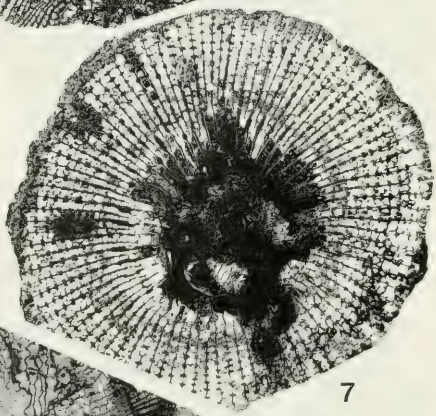
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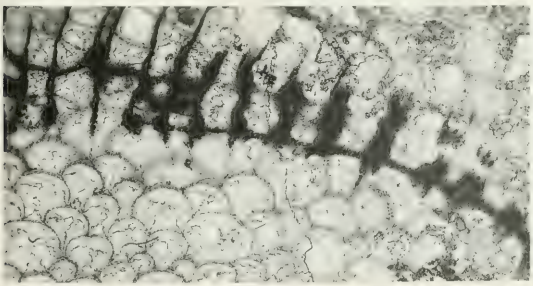
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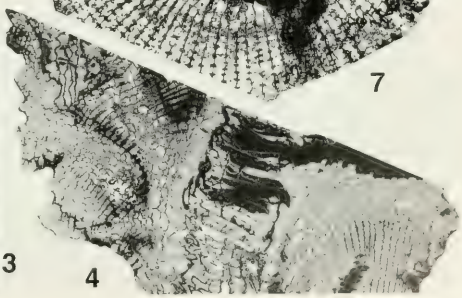
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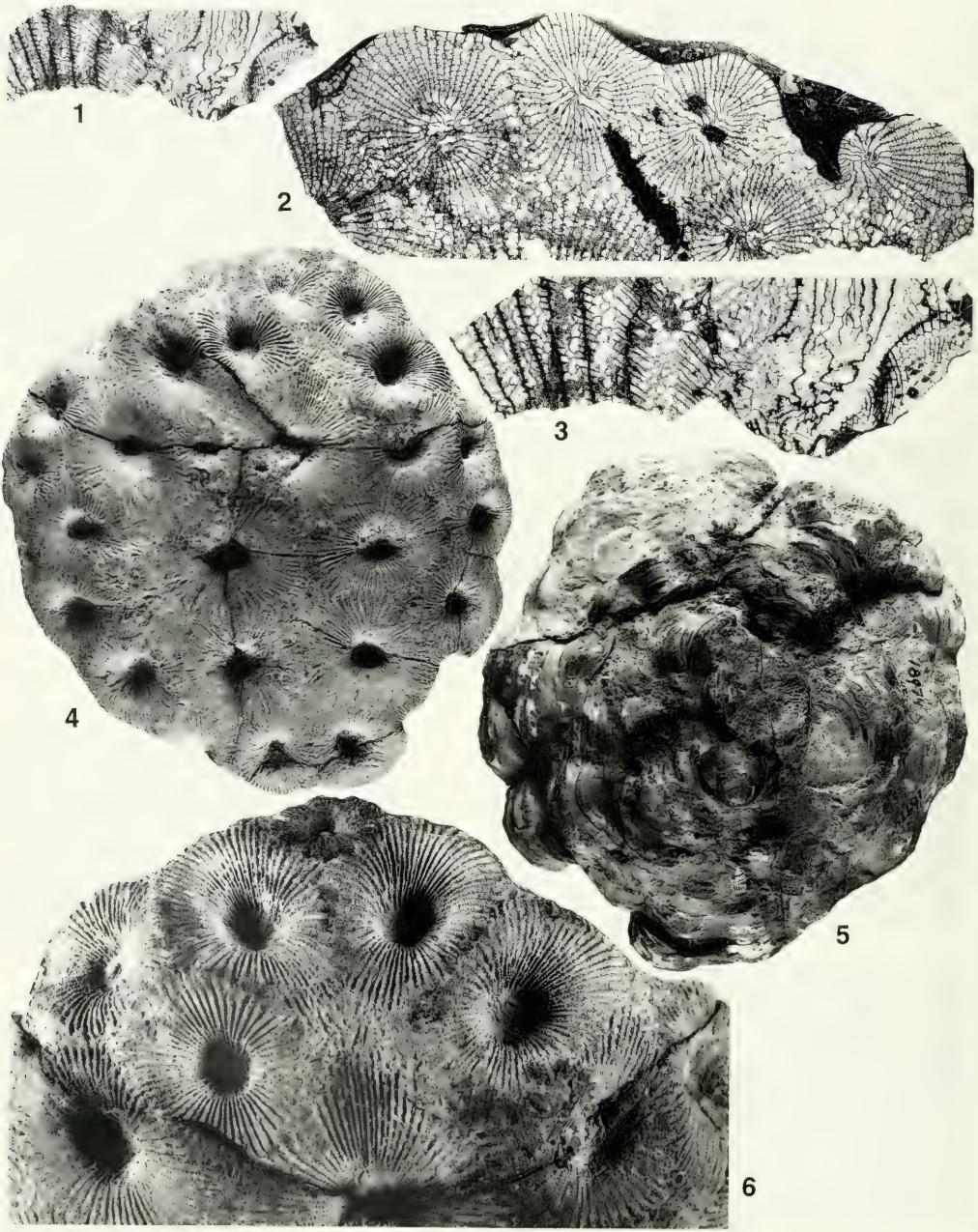
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## EXPLANATION OF PLATE 14

Figure — Page

1–6. ***Heliophyllum halli confluens*** (Hall); FMNH UC 18974, Lectotype, original of Hall (1877, pl. 17); York, Livingston County. Assumed to be from Greens Landing coral bed, Jaycox Member, along Browns Creek, west of York (associated with our population 7). 1–3. thin sections taken from the underside of the part of the colony toward the top of the plate in figures 4–6 (see also Pl. 15, fig. 7); 1, 2. longitudinal and transverse (UD) sections (×1.5); 3. same as figure 1 (×2.5); 4, 5. upper and lower surfaces of corallum (×0.5) with the same part of specimen toward the top of plate; 6. part of upper surface (×1) removed and cleaned by E.C. Stumm in preparation for his study (1955); this is uppermost in figure 4 but here is tilted slightly toward the camera for better detail. . . . 24

## EXPLANATION OF PLATE 15

Figure — Page

1–9. ***Heliophyllum halli confluens*** (Hall); Greens Landing coral bed, Jaycox Member (associated with population 7); . . . . . 24

1, 2. USNM 518542; Locality USGS 5323-SD, west of York; top surface of corallum (×1) and transverse section just below (×1.5).

3, 4. USNM 487252, "East Bethany, N.Y." (×1); top and side views of twins(?), may have been product of fusion of two larvae.

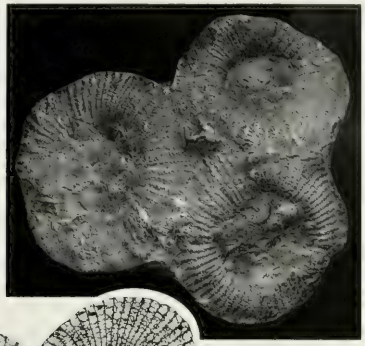
5, 6. AMNH 517241, Paralectotype, original of Hall (1877, pl. 26, figs. 3, 4); Genesee Valley, N.Y. (AMNH catalog); upper and lower surfaces of corallum (×1) composed of 7 or more corallites.

7. FMNH UC 18974, Lectotype, see explanation of Plate 14; part of transverse section (UD) shown on Plate 14, figure 2 (×5).

8. USNM 518543, USGS 5323-SD, west of York; part of transverse section (×1.5).

9. USNM 518544, USGS 5703-SD, Alden; part of transverse section (×1.5).

Specimens without USGS collection numbers are assumed to be from the Greens Landing coral bed because the subspecies is known only from this unit. Figures 7, 8, and 9 are to illustrate boundaries between corallites.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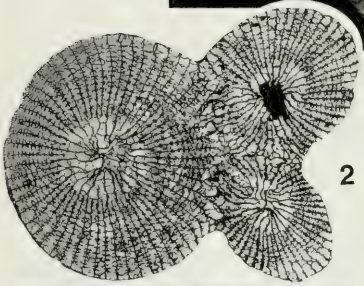
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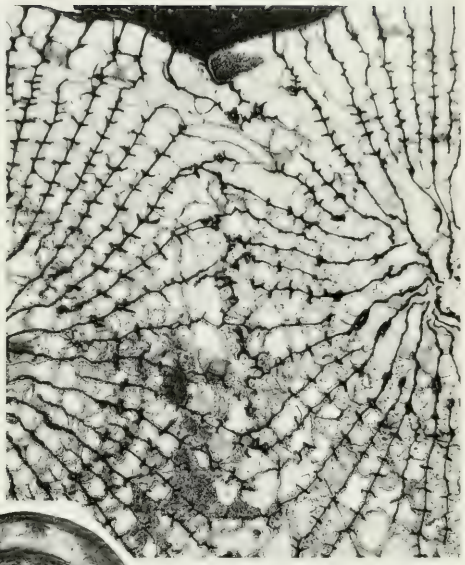
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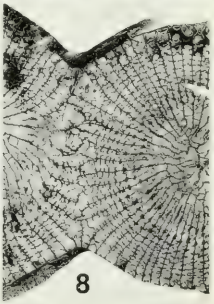
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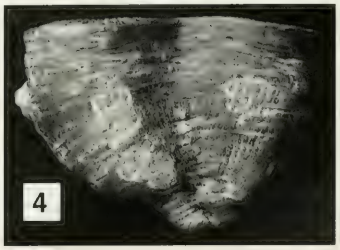
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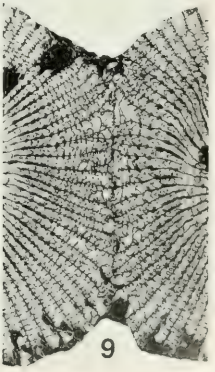
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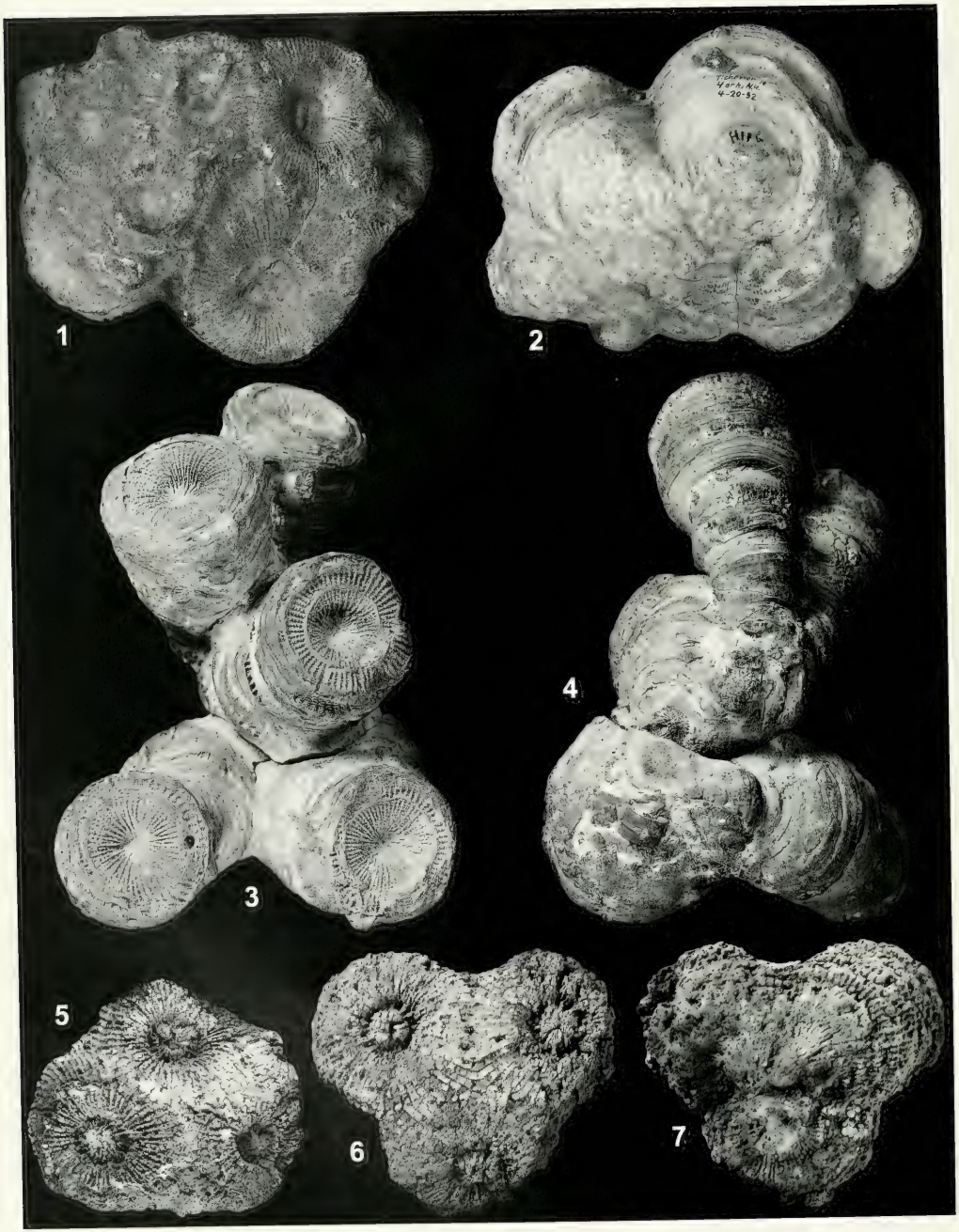
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## EXPLANATION OF PLATE 16

Figure — Page

1–4. ***Heliophyllum halli confluens*** (Hall); Greens Landing coral bed, Jaycox Member (associated with population 7); . . . . . 24

1, 2. USNM 518545; collection USGS 11196-SD, west of York; upper and lower surfaces of corallum with 10 or more corallites (×0.66).

3, 4. USNM 518546; East Avon, collected, prepared, and given to USNM by G. Kloc; corallum with astreoid stage succeeded by separate, continued growth of 5 corallites (×1).

5–7. ***Heliophyllum halli*** cf. ***H. halli confluens*** (Hall); Prout Limestone, Bloomingville, Ohio; two coarsely silicified triplets (×1); . . . . 24

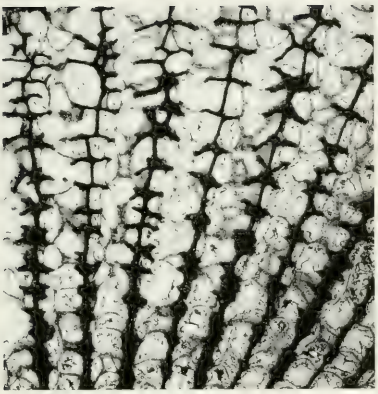
5. USNM 518547; upper surface.

6, 7. OCGM 6085; upper and lower surfaces; illustrated by Stumm (1942, pl. 82, fig. 16).

## EXPLANATION OF PLATE 17

Figure — Page

1–3. ***Heliophyllum halli confluens*** (Hall); sections illustrating Type III carinae; USNM 518548 (see also Pl. 18); Greens Landing coral bed, Jaycox Member (associated with population 7), USGS 5323-SD, west of York; 1, 2. parts of transverse (UD) and longitudinal sections (×10); 3. part of same longitudinal section (×50). . . . . 24



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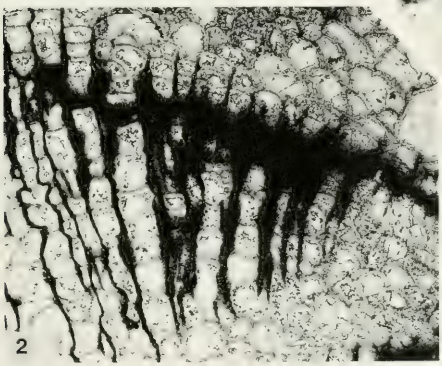

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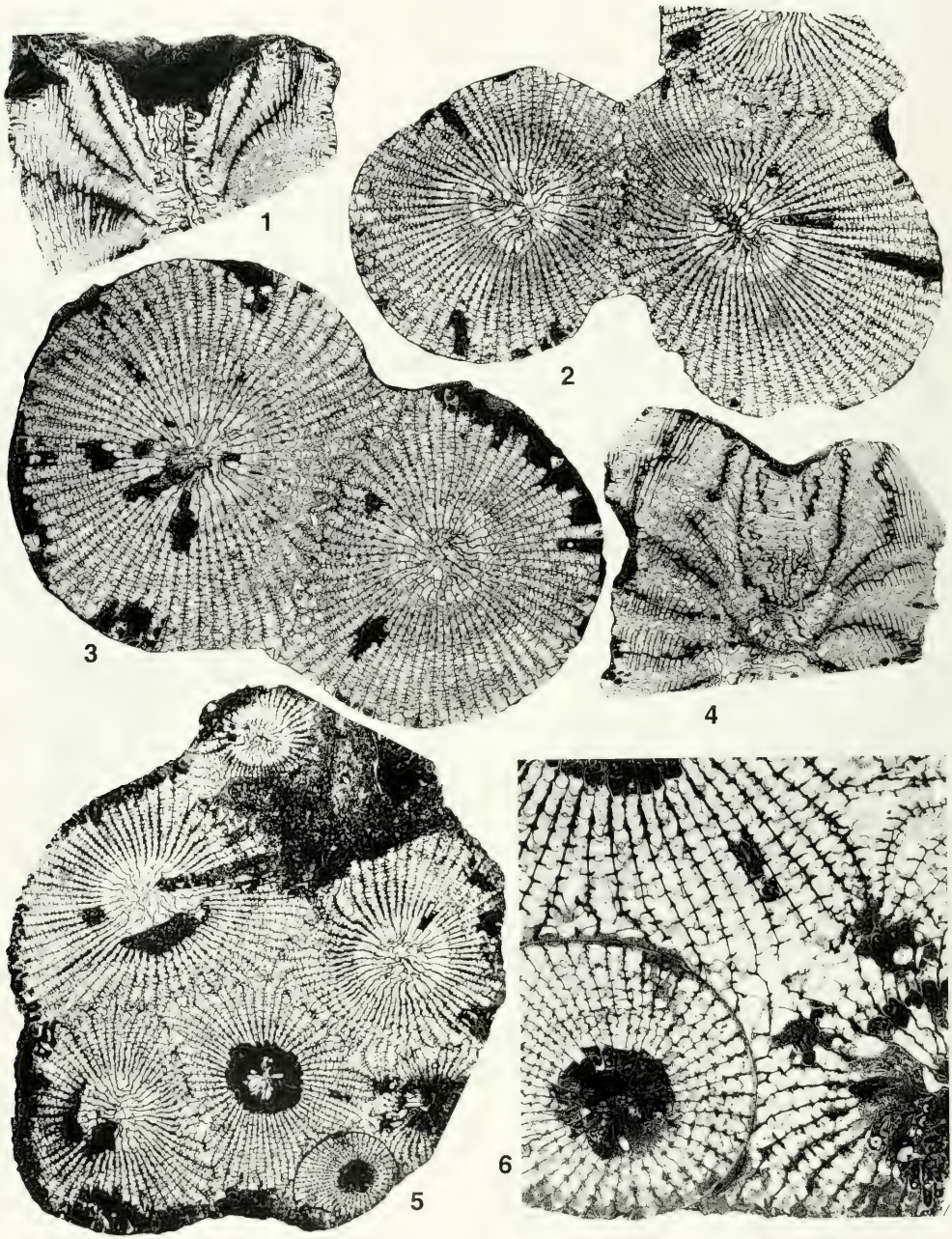
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## EXPLANATION OF PLATE 18

Figure Page

1–6. ***Heliophyllum halli confluens*** (Hall); Greens Landing coral bed, Jaycox Member (associated with population 7); . . . . . 24

1–4. USGS 5323-SD, west of York. 1, 2. USNM 518548 (see also Pl. 17); longitudinal and transverse sections of triplet (×1.5). 3, 4. USNM 518549; transverse and longitudinal sections of twin (×1.5).

5, 6. USGS 5708-SD, Bullis Bridge; USNM 518550 (see also Pl. 19); transverse section (×1.5) and detail of same (×5) in corallum of 7 or more corallites, showing cerioid-type wall bounding one small corallite, possibly a young offset at the margin of the colony.

## EXPLANATION OF PLATE 19

Figure Page

1–5. ***Heliophyllum halli confluens*** (Hall); Greens Landing coral bed, Jaycox Member (associated with population 7); . . . . . 24

1. USNM 518550, USGS 5708-SD, Bullis Bridge; detail of transverse section in Plate 18, figure 5 (×10).

2–5. USNM 518551, USGS 5323-SD; 2, 5, longitudinal and transverse sections of corallum with three or more corallites (×1.5); 3, 4, details of section in figure 2; 3 (×5), showing contact between two corallites in longitudinal section; 4 (×10), showing Type III carinae (right side of right-hand corallite).

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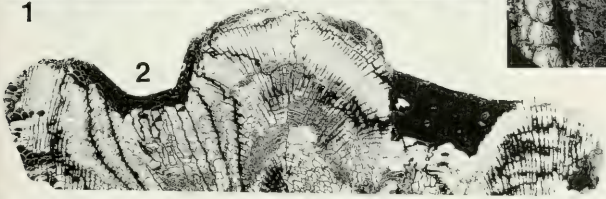

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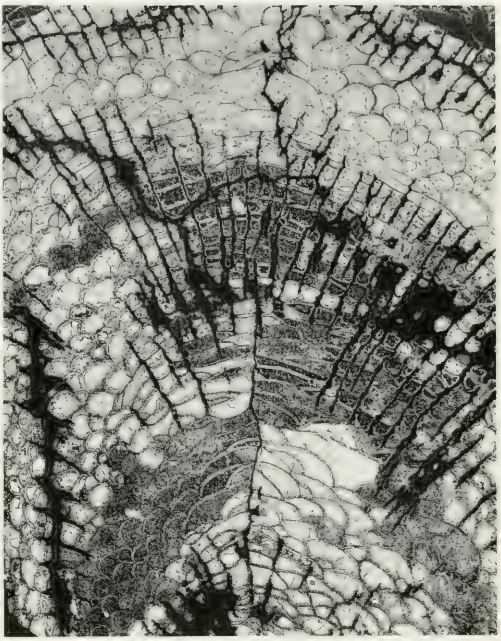

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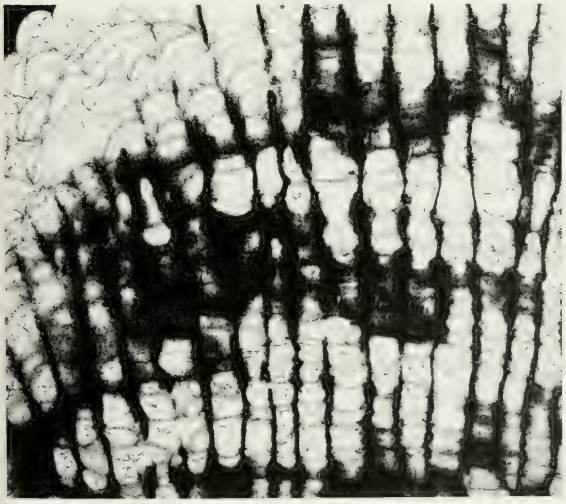

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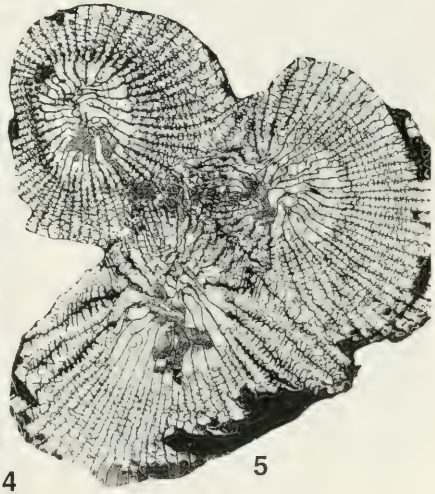

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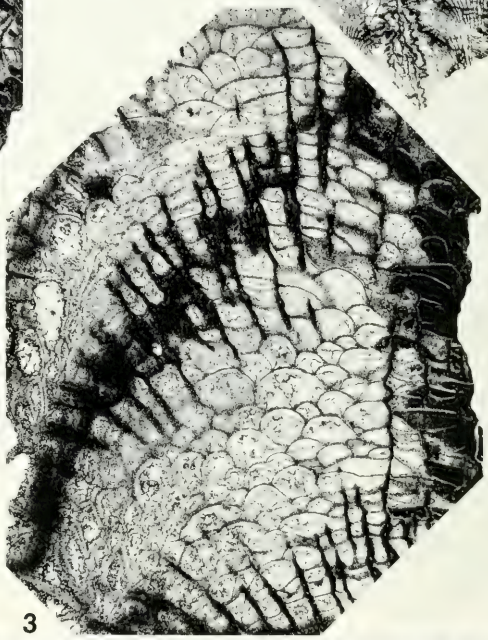
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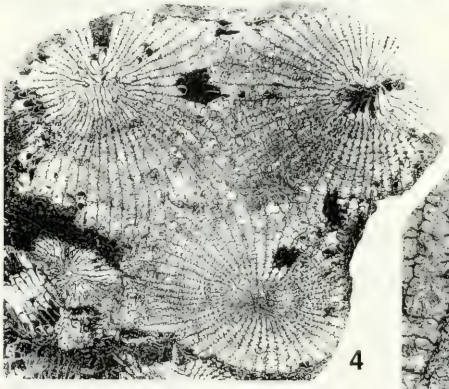
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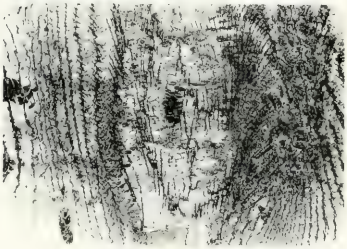
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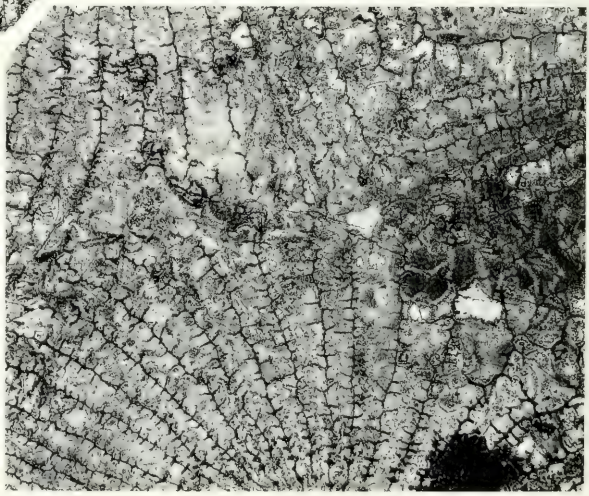
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## EXPLANATION OF PLATE 20

Figure Page

1–6. ***Heliophyllum halli bellonense*** n. subsp.; Bellona coral bed, Tully Limestone (associated with population 10); . . . . . 26

1–3. Paratype, USNM 518561; Scipio Town Quarry, collected by J.W. Wells; longitudinal section (×1.5) and details of same (×5, ×10), showing Type III and I→III carinae.

4–6. Holotype (herein designated), USNM 518562, USGS 5341-SD, Bellona; collected and given to USNM by P. H. Heckel; transverse and longitudinal sections (×1.5) and detail of transverse (×5).

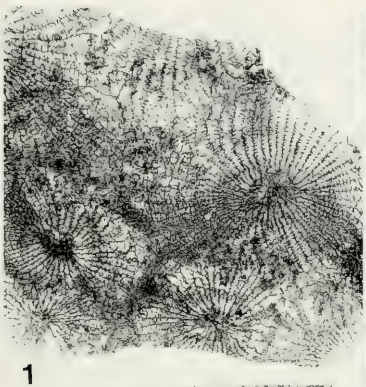
## EXPLANATION OF PLATE 21

Figure Page

1–5. ***Heliophyllum halli bellonense*** n. subsp.; Bellona coral bed, Tully Limestone (associated with population 10); collected and given to USNM by P. H. Heckel . . . . . 26

1–3. Paratype, USNM 518563, Bellona; transverse and longitudinal sections (×1.5) and detail of transverse (×5); note crushing of marginal parts of corallites.

4, 5. Paratype, USNM 518564, Twelve Corners, Owasco Quad.; transverse section (×1.5) and detail (×5).



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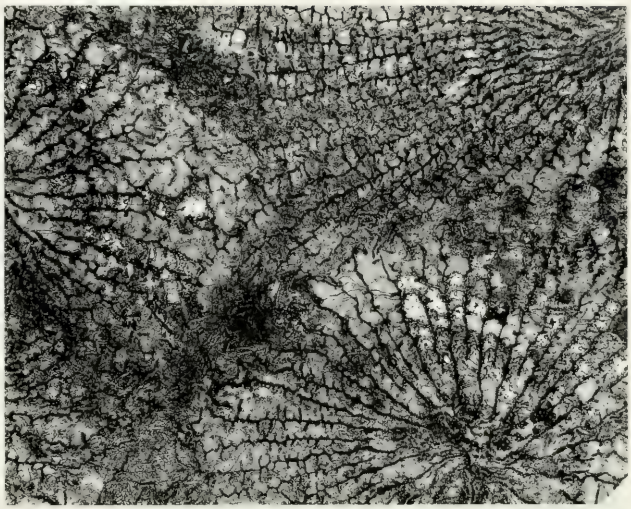

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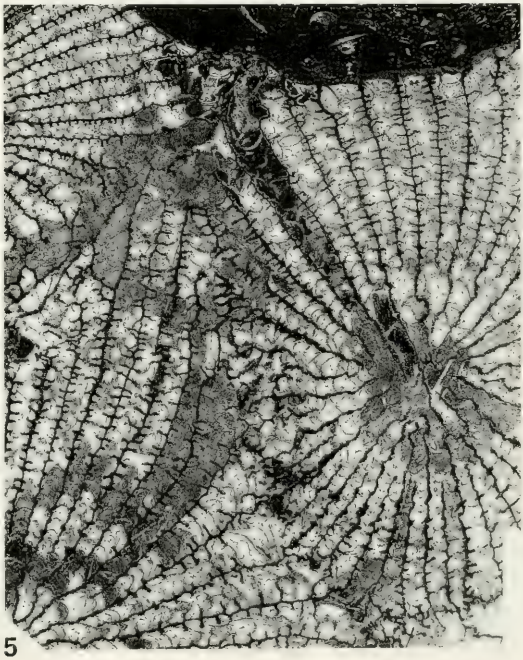

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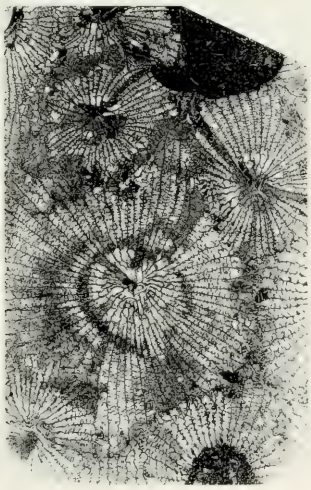

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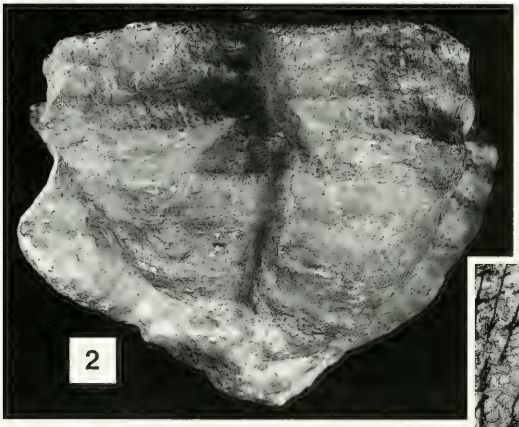
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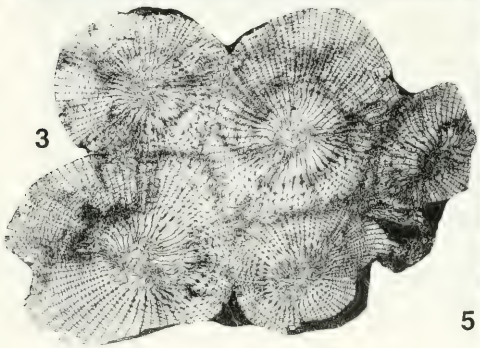
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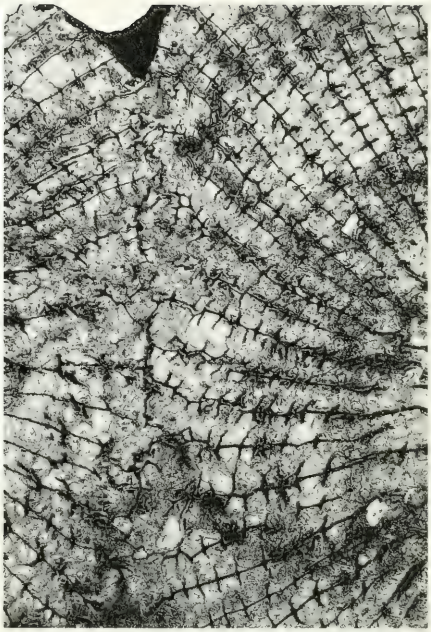
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## EXPLANATION OF PLATE 22

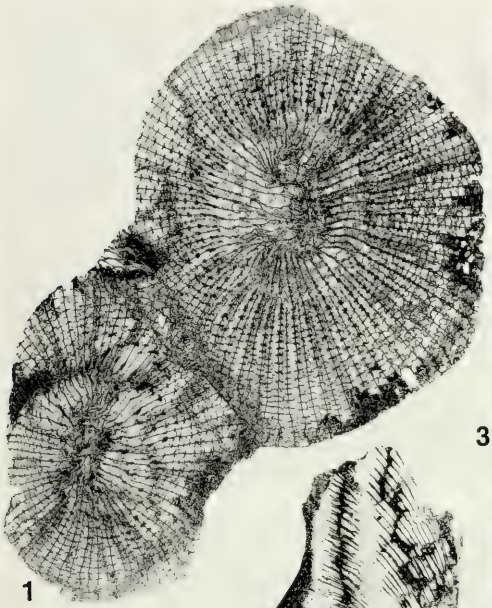
Figure Page

1–5. ***Heliophyllum halli joshuense*** n. subsp. (form A); Joshua coral bed (associated with population 5). Holotype (here designated), PRI 24560, Lords Hill (*H. confluens* of Wells, 1937, text-fig. 8); 1, 2. exterior views of upper surface and side (×1); the latter is the aspect outlined by Wells in his figure 8. 3–5. transverse section (×1) and two details (×5) showing general nature of carinae and contact zones between corallites; short segments of the cerioid wall are seen in figure 4. . . . . 27

## EXPLANATION OF PLATE 23

Figure — Page

1–5. ***Heliophyllum halli joshuense*** n. subsp. (form A); Joshua coral bed (associated with population 5). Paratype, USNM 518568, USGS 8783-SD, Lords Hill cornfield. 1, 2. transverse and longitudinal sections (×1.5). 3. detail of transverse section (×5) showing incomplete cerioid wall between corallites. 4, 5. details of longitudinal section (×10, ×5) with Type III carinae. . . . . 27



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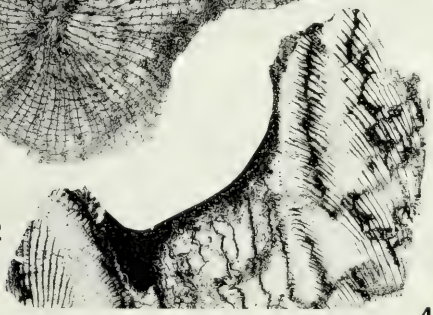

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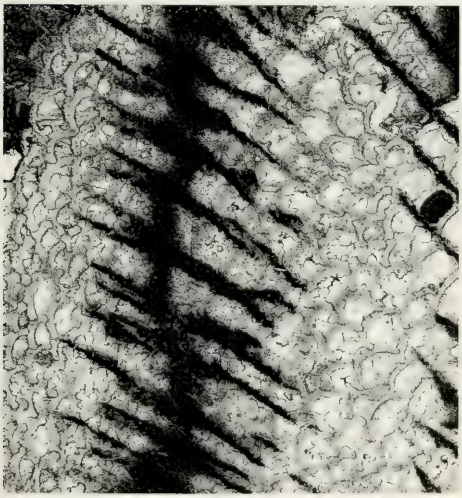

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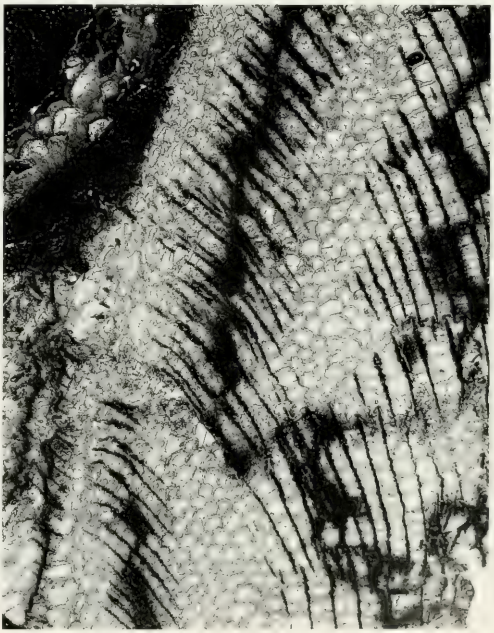

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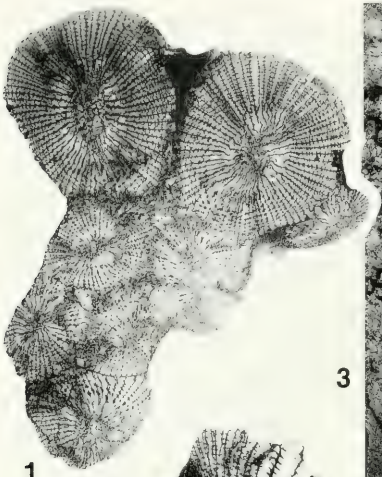

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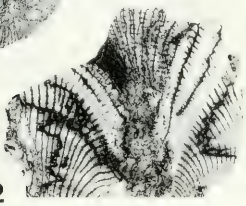

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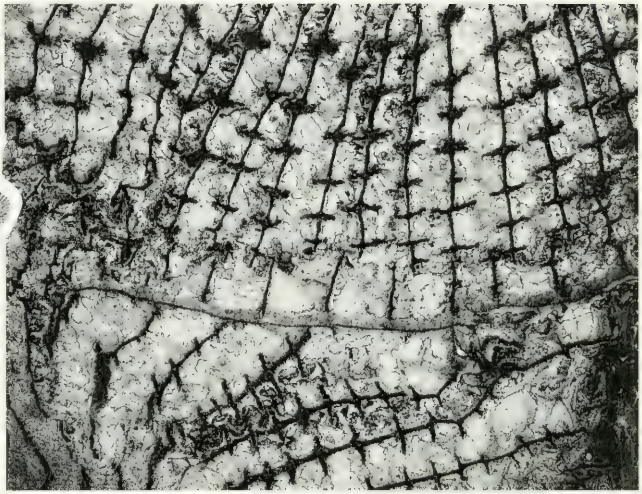

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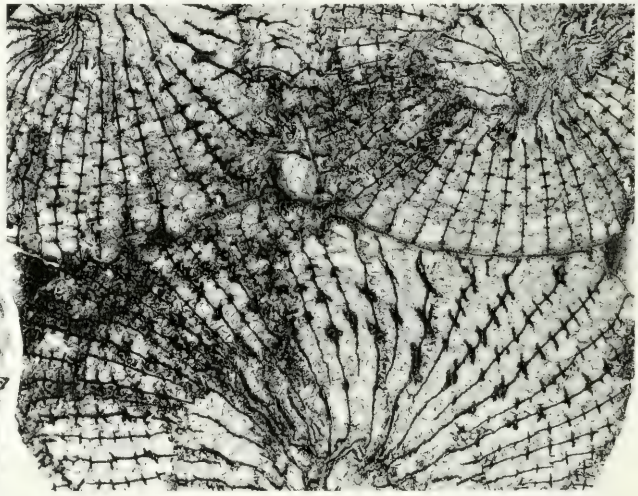

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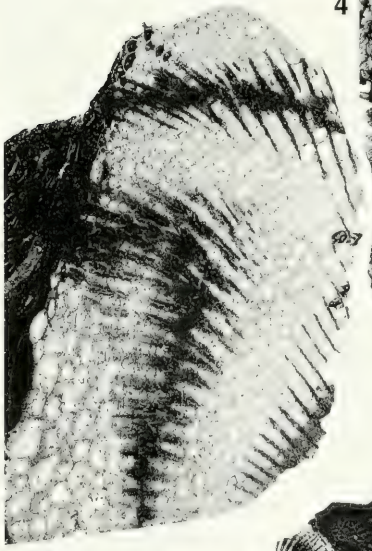

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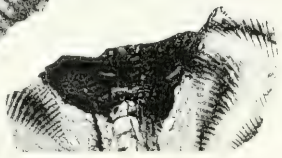

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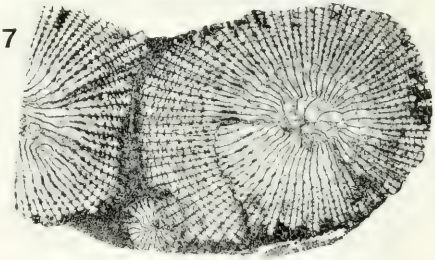

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## EXPLANATION OF PLATE 24

Figure Page

1–7. ***Heliophyllum halli joshuense*** n. subsp. (form A); Joshua coral bed (associated with population 5), USGS 8783-SD, Lords Hill cornfield. . . . . 27

1–4. Paratype, USNM 518569; 1, 2. transverse and longitudinal sections of corallum with 8 or more corallites (×1.5); 3, 4. details (×10, ×5) of transverse section showing nearly complete cerioid wall between corallites in upper right and lower parts of figure 1.

5–7. Paratype, USNM 518570; 6, 7. longitudinal and transverse sections (×1.5); 5. detail (×5) of longitudinal section showing Type III carinae.

## EXPLANATION OF PLATE 25

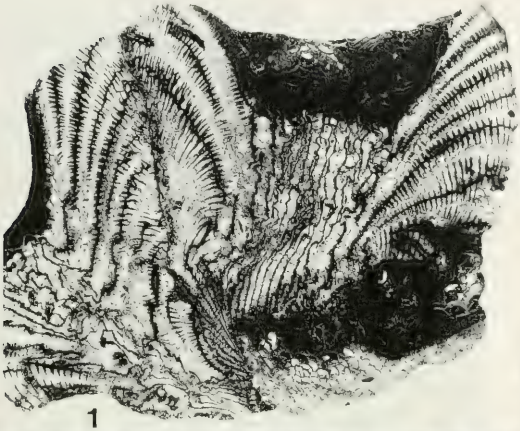
Figure Page

1–6. ***Heliophyllum halli joshuense*** n. subsp. (form A); Joshua coral bed (associated with population 5), USGS 8762-SD, Lords Hill cornfield. . . . . 27

1, 2. Paratype, USNM 518571; longitudinal section (×1.5) and detail (×5) of twin showing intercorallite cerioid-type wall and Type III carinae.

3, 4. Paratype, USNM 518572; transverse section (×1.5) and detail (×10) of twin showing very incomplete intercorallite wall.

5, 6. Paratype, USNM 518573; longitudinal section (×1.5) and detail (×5) of corallum with 4 corallites showing nearly complete wall between two of them.



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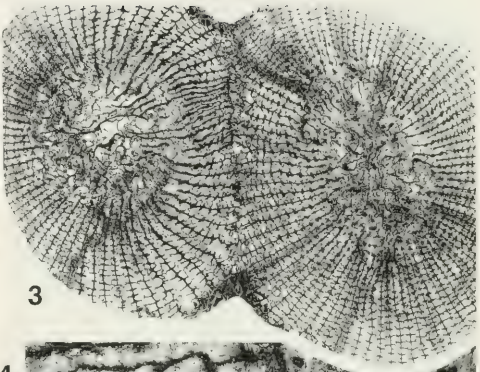

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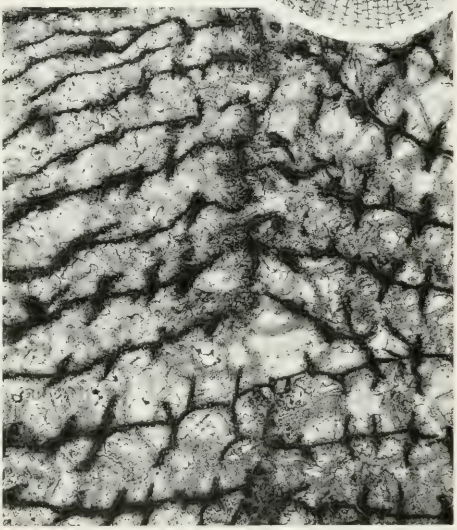

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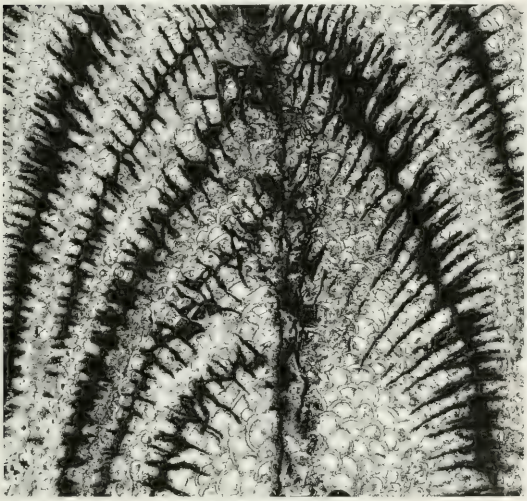

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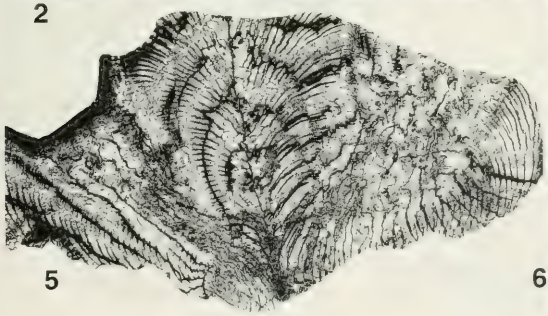

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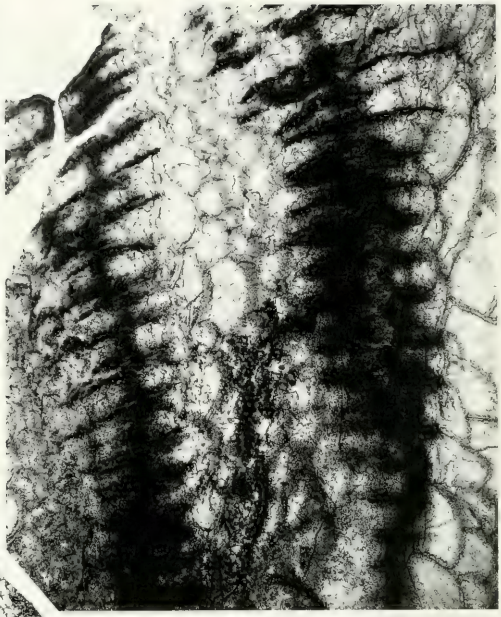
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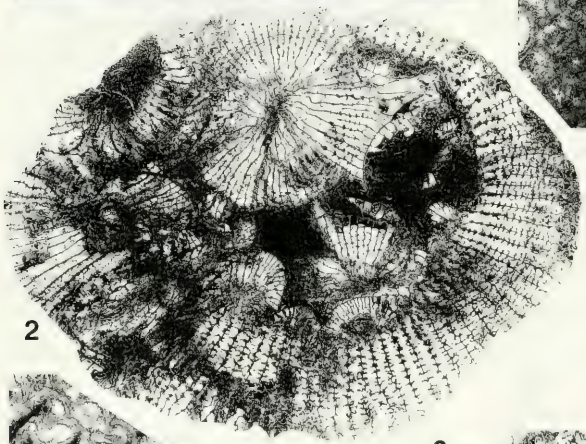
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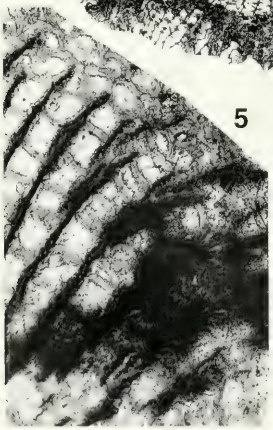
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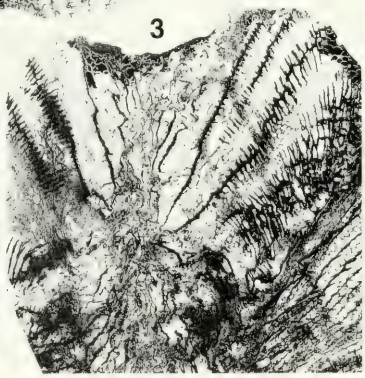
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## EXPLANATION OF PLATE 26

Figure — Page

1–6. ***Heliophyllum halli joshuense*** n. subsp. (form B); Joshua coral bed (associated with population 5); Paratype, USNM 518574, USGS 8762-SD, Lords Hill cornfield; 1. exterior (top) view of corallum (×0.67); corallites in this view are distal ends of the offsets seen in figure 2; 2. transverse section (×1.5) showing 8 or more peripheral offsets within calice of large turbinate protocorallite; section is from approximately 5 cm below the highest point on the top surface in figure 1; 3–6. longitudinal section (×1.5) of an offset (position of cut can be seen in fig. 1) and details (×10, ×10, ×5) to show Type III carinae. . . . . 27

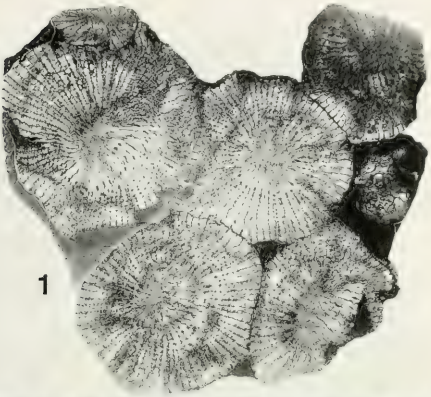
## EXPLANATION OF PLATE 27

Figure — Page

1–7. ***Heliophyllum halli joshuense*** n. subsp. (form B); Joshua coral bed (associated with population 5), USGS 5667-SD, SW side of Otisco Lake. . . . . 27

1–3. Paratype, USNM 487758; 1, 2. transverse section (×1) and detail (×5) of semiphaceloid corallum with 6 or more corallites; detail, showing intercorallite cerioid wall, is from upper right part of figure 1; 3. part of longitudinal section (×5) with Type I→III carinae.

4–7. Paratype, USNM 518575 (see also Pl. 28); 4. longitudinal section (×1.5) from above the transverse sections on this and Plate 28; 5. transverse section (×1.5) of apparent protocorallite with 12(?) peripheral offsets; 6. detail (×25) of protocorallite septa in figure 5 (at 6 o'clock position); 7. detail (×5) of some of the offsets in figure 5; note that some of the septa connect through the crush zone; the section in figures 5–7 is approximately 15 mm below the next higher section shown on Plate 28 (fig. 2).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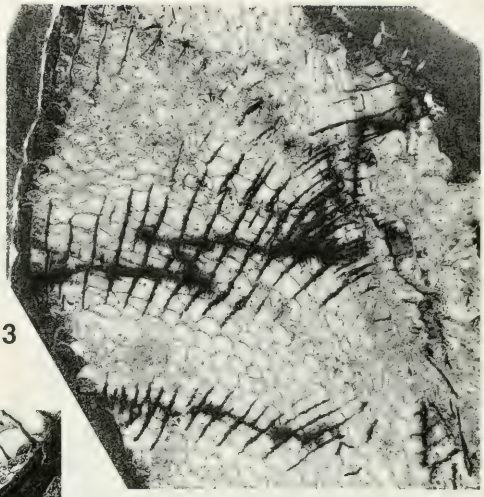
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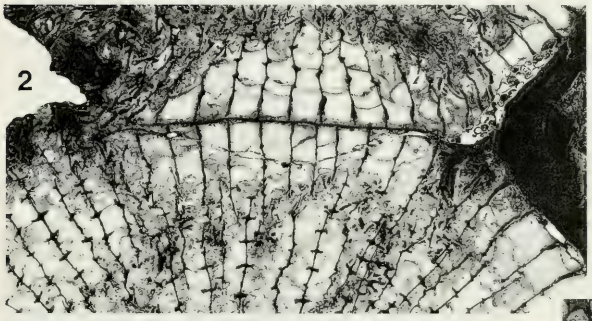
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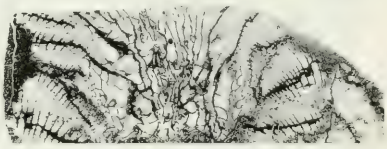
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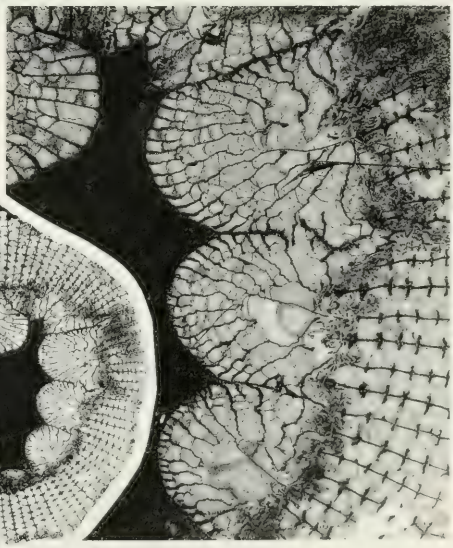

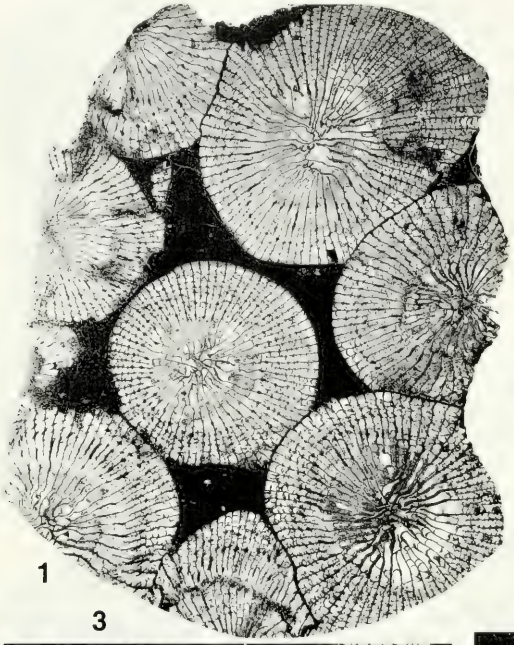

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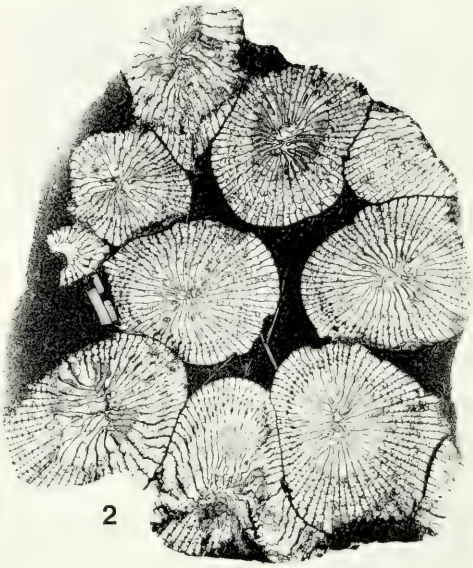

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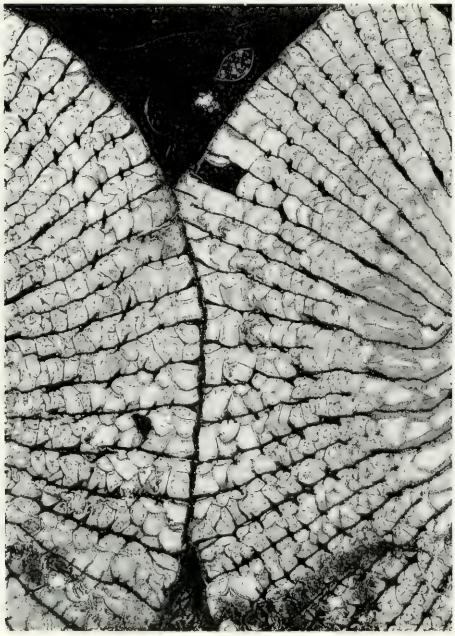

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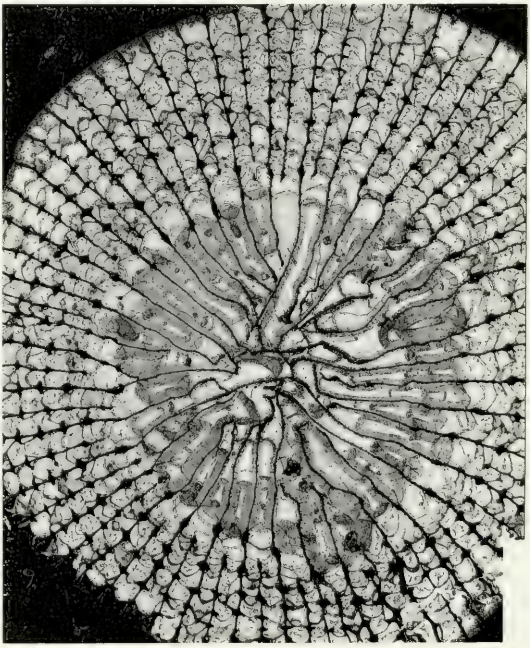

## EXPLANATION OF PLATE 28

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1–4. ***Heliophyllum halli joshuense*** n. subsp. (form B); Paratype, USNM 518575 (see also Pl. 27), USGS 5667-SD, Joshua coral bed (associated with population 5), SW side of Otisco Lake. 1, 2. transverse sections (×1.5); the section in figure 2 is parallel to and approximately 15 mm above the section in Plate 27, figure 5; the section in figure 1 is some 10 mm higher than that in figure 2; 3, 4. details of section in figure 1 (×5); 3. cerioid intercorallite wall between corallites in upper right; 4. center corallite showing dilation of major septa in tabularium. . . . . 27

## EXPLANATION OF PLATE 29

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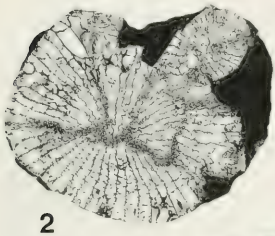
1–7. ***Heliophyllum delicatum*** Oliver and Sorauf, 1994. . . . . 28

1–5. Holotype (by original designation), USNM 474690, Canandaigua Lake, locality 9 of Oliver and Sorauf (1994, p. 1201). 1, exterior view of large colony from above (×0.2); 2, 3, transverse sections (×1.5) from immediately above and below longitudinal section in figure 5; 4, detail (×10) of upper part of transverse section in figure 3; 5, longitudinal section (×4) between the two transverse sections in figures 2 and 3; note predominance of Type I carinae.

6. Paratype, USNM 474709, Alden, locality 2 of Oliver and Sorauf (1994, p. 1200). Longitudinal section (×1.5) showing Type I carinae.

7. Paratype, USNM 474715, Honeoye quad., locality 8 of Oliver and Sorauf (1994, p. 1200). Exterior of corallum lying on bedding plane (×0.5).

All figures except 6 after Oliver and Sorauf (1994).



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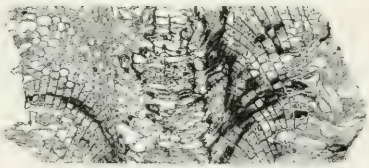

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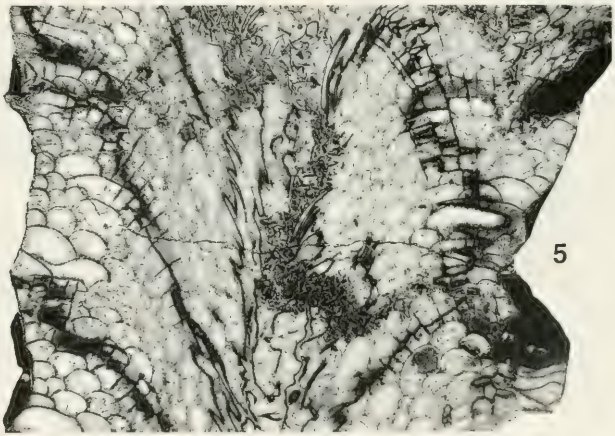

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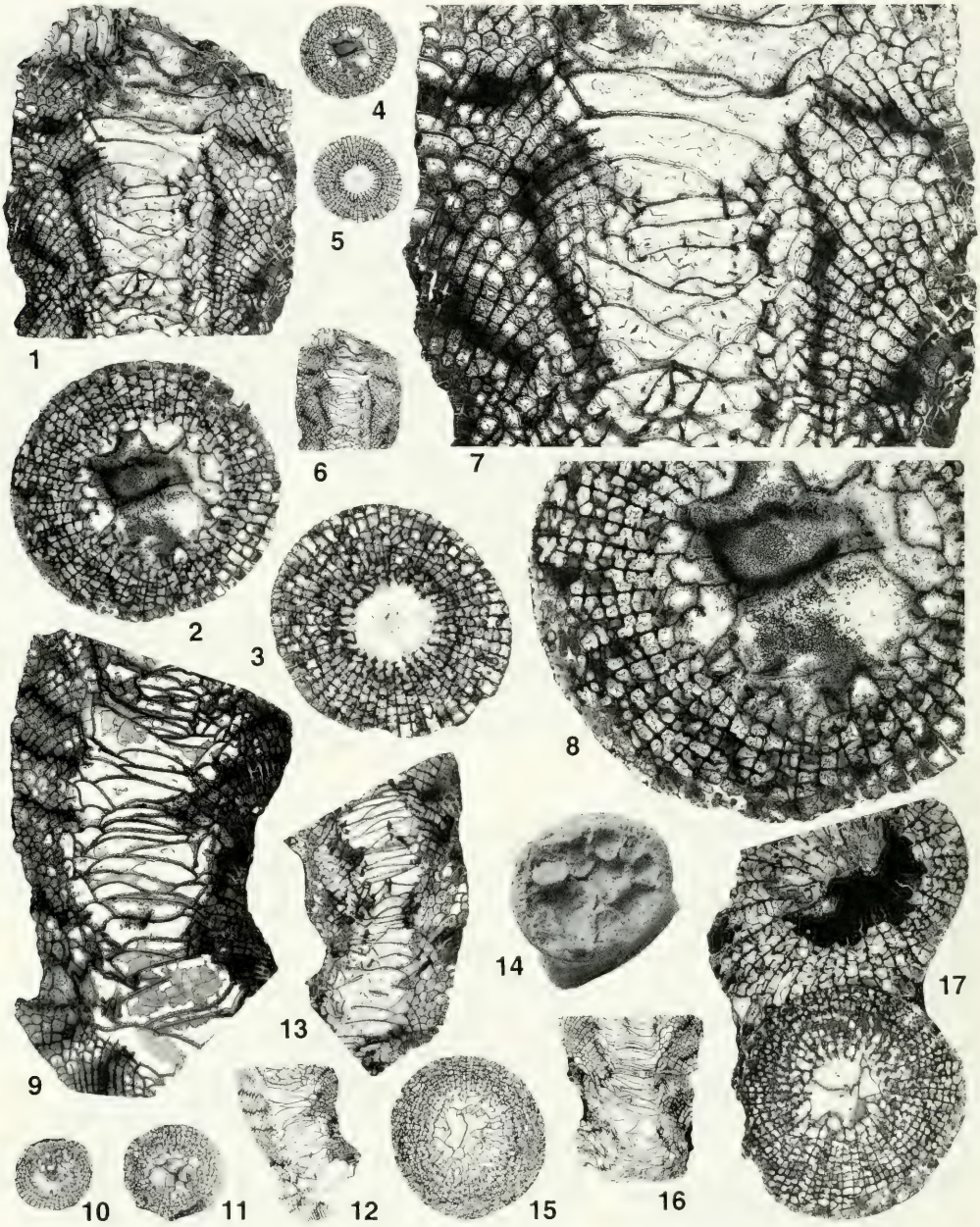
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## EXPLANATION OF PLATE 30

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1–17. ***Heliophyllum cribellum*** n. sp.; Centerfield Limestone, associated with *H. halli halli* population 4; USGS 4678-SD, East Alexander. . . . . 29

1–8. Holotype, here designated, USNM 518586; medium sized, ceratoid-cylindrical form. 1–3. longitudinal and two transverse sections (×4); the transverse sections are from below the longitudinal and were separated by approximately 4 mm. 4–6. the three sections in figures 1–3 (×1.5) for comparison with our standard *H. halli* photos. 7, 8. parts of sections in figures 1 and 2 (×8); 7. showing simple Type I carinae; 8. long yard-arm carinae.

9–12. Paratype, USNM 518587, medium sized, ceratoid-cylindrical form showing rejuvenation; 9. longitudinal section (×4); 10–12. lower and upper transverse sections and intervening longitudinal section (×1.5).

13. Paratype, USNM 518588, medium sized, ceratoid-cylindrical form; longitudinal section (×4).

14–16. Paratype, USNM 518589, large ceratoid form. 14. top view of calice with 7 peripheral offsets (×1.5). 15, 16. transverse section from below calice and lower longitudinal section (×1.5).

17. Paratype, USNM 518590, small *H. cribellum* partly overgrown by an *H. halli halli* (×4).

## EXPLANATION OF PLATE 31

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1–16. ***Heliophyllum cribellum*** n. sp.; Centerfield Limestone, associated with population 4 of *H. halli halli*. . . . . 29

1–3. Paratype, USNM 518591, USGS 11210-SD, Center Road; large ceratoid-cylindrical form. 1. part of transverse section with long yard-arm carinae (×5); 2, 3. longitudinal section (×1.5) and part of same showing bushy, Type I carinae (×7).

4, 5. Paratype, USNM 518592, USGS 4678-SD, East Alexander; small, trochoid form; transverse and longitudinal sections (×1.5).

6, 7. Paratype, USNM 518593, USGS 11211-SD, Jaycox Run; large ceratoid form; longitudinal section (×1.5) and transverse section with typical "screen" appearance (×4).

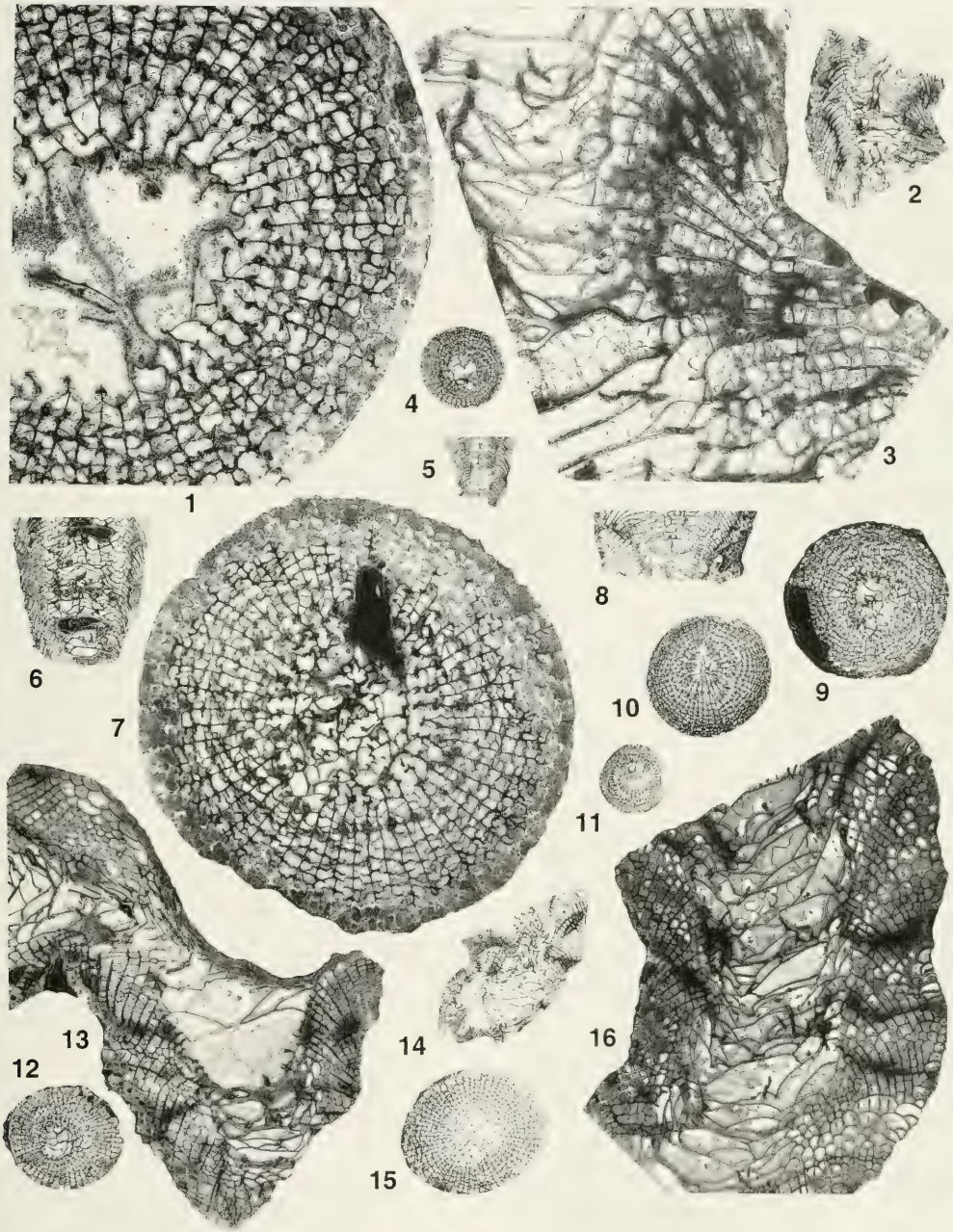
8, 9. Paratype, USNM 518594, USGS 11468-SD, Schaeffer Creek; large ceratoid form; longitudinal and transverse sections (×1.5).

10, 11. Paratype, USNM 518595, USGS 5692-SD, White Creek; trochoid form; upper and lower transverse sections, approximately 15 mm apart (×1.5).

12, 13. Paratype, USNM 518596, USGS 4678-SD, East Alexander. 12. transverse section (×1.5); 13. longitudinal section showing sequence of trochoid growth, trauma, rejuvenation and further growth at right angle to initial growth direction (×3.5); transverse section in figure 12 is from below calice in final stage (upper left in fig. 13).

14, 15. Paratype, USNM 518597, USGS 11197-SD, east of York; medium sized, ceratoid form; longitudinal and transverse sections (×1.5).

16. Paratype, USNM 518598, USGS 4678-SD, East Alexander; ceratoid-cylindrical form; longitudinal section (×4).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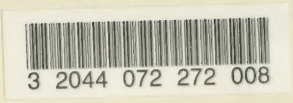


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